## The Conus cedonulli complex: Historical review, taxonomy and biological observations

by

Danker L. N. VINK \* and Rudo von COSEL \*\*

With 12 plates and 10 figures

#### ABSTRACT

A history of previous investigations of the Conus cedonulli complex is given, with comments on the reviews by LINNÉ (1758 and 1767), HWASS (1792), MARTINI and CHEM-NITZ (1773-1788), SCHUBERT & WAGNER (1829), KÜSTER & WEINKAUFF (1837-1875), REEVE (1843), KIENER (1845-1850), SOWERBY II (1857), MERMOD (1947) and VINK (1977). Within the complex, 8 closely related species are recognized: the recent C. cedonulli Linné, 1767, C. pseudaurantius n. sp., C. aurantius Hwass in Bruguière, 1792, C. mappa Lightfoot, 1786, C. curassaviensis Hwass in Bruguière, 1792, C. archon Broderip, 1833, and C. scopulorum van Mol, Tursch & Kempf, 1971, and the fossil C. consobrinus Sowerby I, 1850. C. cedonulli from oceanic islands in the Eastern Caribbean (Lesser Antilles) and C. mappa from the continental shelf of northern South America have developed various populations in different geographic areas. These populations have constant differences in colour and pattern and therefore are here treated as subspecies, i.e. C. cedonulli cedonulli, C. cedonulli insularis Gmelin, 1791, C. cedonulli dominicanus Hwass in Bruguière, 1792, C. mappa mappa, C. mappa trinitarius, Hwass in Bruguière, 1792 and C. mappa granarius Kiener, 1848. Furthermore there exist colour varieties, to which various names have been given, such as "C. caledonicus" Hwass in Bruguière, 1792 and "C. holemani" Usticke, 1968. For each taxon synonymy, differential characters and information on distribution and habitat are provided. A statistical analysis of the morphometric parameters shell length (SL), maximum diameter (MD) and aperture height (AH) is presented.

<sup>\*</sup> Prinsenweg 73, Wassenaar, The Netherlands.

<sup>\*\*</sup> Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Hamburg, BRD, and Muséum national d'Histoire naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, Paris, France.

The cones of the *Conus cedonulli* complex inhabit soft bottoms except mud in the vicinity of hard substrate between 1.5 and 160 m. They mostly feed on polychaetes of the family Amphinomidae.

Metamorphosis takes place within the egg capsule, the youngs have a paucispiral embryonic shell and hatch at least in the late pediveliger stage; there is no planctonic phase.

The Conus cedonulli group is a species and subspecies complex with mostly allopatric members at various stages of speciation, presumably originating from a common ancestor and now separated by biological barriers.

#### I. HISTORICAL REVIEW OF PREVIOUS INVESTIGATIONS

Information on the history of investigations of the Conus cedonulli complex was provided already by DANCE (1966: 232-235), more briefly by DUNN (1971) and VINK (1977; 1982), and finally by COOMANS, MOOLENBEEK & WILS (1983). Because of their beauty and extreme rarity the cones belonging to the C. cedonulli group have been known since the 18th century. There is evidence from pre-linnean common names that these cones were originally referred to as "admiral cones", because the pattern of some specimens of C. cedonulli cedonulli Linné, 1767 with strings of white dots on a golden yellow background is reminiscent of the sleeve stripes of an admiral consisting of five golden bands stitched together to form a solid band. From d'ARGENVILLE (1757: 384) "Le fameux admiral nommé par excellence cédonulli", it can be concluded that already in the early times of conchology for the most beautiful cone of the group the name cedonulli was used, "cedo nulli" meaning "I am second to none", more freely translated "(cone) yielding to nothing" or "the matchless (cone)". According to HWASS in BRUGUIÈRE (1792), KLEIN (1753) first referred to Conus cedonulli as a species, but the name Conus cedonulli in the "Encyclopédie Méthodique" is not attributed to an author in the general heading of the C. cedonulli chapter. KLEIN is cited only as author of Conus cedonulli under "A — Cedonulli amiralis".

Taxonomically available names first appear in Carl von LINNÉ's Systema Naturae with 4 infraspecific taxa of *Conus ammiralis: C. a. summus, C. a. ordinarius* and *C. a. occidentalis* in the 10th edition (1758: 713-714) and *C. ammiralis cedo nulli* in the 12th edition (1767: 1167), from "O. Americae meridionalis", with very brief descriptions only. According to Coomans, Moolenbeek & Wils (1983: 102-103), Linné "did not have a specimen in his collection...", so we must assume that Linné's description of *C. ammiralis cedonulli* is based on the cited figure in Seba (175) only. Kohn (1963) selected as lectotype of *C. ammiralis* a specimen in the Linnean collection known to occur in the Indopacific, concluding that the type locality "O. Americae meridionalis" is erroneous, and that the subspecies names given by Linné denote forms of infrasubspecific rank. Thus Kohn's designation definitely establishes *Conus ammiralis* Linné, 1758 as a valid indopacific species, not related to the *Conus cedonulli* complex.

The next survey on cones of the *C. cedonulli* complex with validly proposed taxa appeared in Hwass in Bruguière (1792: 602-606; 634-635). It consists of detailed descriptions of 9 infraspecific taxa of *C. cedonulli*, with the specification that the true *cedonulli* ("le vrai cédonulli") is *C. cedonulli amiralis*, and of the 2 separate species *C. aurantius* and *C. caledonicus*. The following literature is cited: Klein (1753), Seba (1759), d'Argenville (1757), Regenfuss (1758), Linné (1767), Knorr (1772), Favanne (1780), Martini (1773) and Schröter (1782) (for details on the "Encyclopédie Méthodique" see Mermod (1947:

155-162), Hanna & Strong (1949: 256-258), Kohn (1959: 369-370) and Kohn (1968: 431-435)). Each taxon is figured in the "Tableau Encyclopédique...". Although the engraving of the cone plates had been ordered already by Hwass, the plates were finally not published by himself, but under the supervision of Lamarck in 1798, "apparently quite independently of Bruguière" (Kohn, 1968: 432). Hwass' descriptions are based on specimens in his own collection. 6 of these, including the holotype of *C. aurantius* and *C. caledonicus*, are still present in the Hwass collection now in the Muséum d'Histoire Naturelle in Geneva. The whereabouts of the remaining specimens are unknown. The 11 taxa of Hwass are listed in table I, together with their present status as here proposed.

HWASS' infraspecific taxa were first fully cited and dealt with by LAMARCK (1822) as "C. cedonulli Lin.".

In the first edition of the "Systematisches Conchylien-Cabinet" by MARTINI & CHEMNITZ figures of cones belonging to the *C. cedonulli* complex were published by MARTINI (Vol. 2, 1773: 4 figs.), CHEMNITZ (Vol. 10, 1788: 2 figs.) and SCHUBERT & WAGNER (Vol. 12, 1829: 4 figs.). In Vol. 2 and Vol. 10 the figures are accompanied by detailed descriptions and "histories" of the figured and other specimens. In Vol. 12, the 9 infraspecific taxa of HWASS are listed with references to most of the pre-linnean works also cited by HWASS, and to BRUGUIÈRE, LAMARCK and Vol. 2 and 10 of the "Conchylien-Cabinet". The descriptions generally are following HWASS' french text, but are more abridged. Among the 4 figured specimens 2 are types of HWASS.

All figures of the first edition appeared again in the cone volume of the second edition by KÜSTER & WEINKAUFF. The first 24 plates, taken from the first edition and only partly changed or redrawn, included all *cedonulli* figures and were published together with the text by KÜSTER in 1837 (pp. 1-24; pls. 1-6) and 1838 (pp. 25-124; pls. A, 7-24) (fide ZILCH, pers. comm.) (the remaining plates 25-71 with text by WEINKAUFF appeared in 1873-75). In KÜSTER's text there are similar descriptions of HWASS' infraspecific taxa as in SCHUBERT & WAGNER, but slightly "modernized", with updated references and under the heading: "Conus cedonulli Klein". C. caledonicus and C. aurantius are monographed separately. The treatment of the C. cedonulli complex in both editions of MARTINI/CHEMNITZ together with the present status of the figured specimens is summarized on table II.

Subsequently, illustrations of cones of the *C. cedonulli* complex were published by DELESSERT (1841: pl. 40). Both sides of the "vrai cédonulli" of LAMARCK are shown, as well as one specimen of the same species from the FAVANNE collection and 7 "variétés du cône cédonulli" from the DELESSERT collection, 4 of these being specimens of HWASS.

REEVE (1843) treated 7 varieties of "C. cedonulli Klein" without systematically relating these with Hwass' names; these are only mentioned in the text. The presumable status of REEVE's varieties is shown in table III. — All foregoing works are cited in the C. cedonulli chapter of LAMARCK, second edition by DESHAYES & MILNE-EDWARDS (1845).

In Kiener (1845-1850), "C. cedonulli Lin." appears besides the separate C. aurantius, C. caledonicus and the newly described C. granarius. 6 varieties of C. cedonulli are illustrated, among these 2 of the Hwass type specimens (C. c. martinicanus and C. c. trinitarius).

CHENU (1847) published figures of cones of the *C. cedonulli* complex, illustrating the same specimens in the same sequence as already figured by DELESSERT (1841). In CHENU (1859) followed a colour plate with figures of "Cône cédonulli et variétés" and with HWASS' infraspecific names, but in the short legends not referring to HWASS himself, but to LAMARCK ("LAMARCK a décrit neuf variétés du cône cedonulli..."). In the text only the name "*C. cedonulli* Linné" is cited, without any discussion of HWASS' names. All speci-

mens figured by Delessert and Chenu, with the exception of one, are present in the Muséum d'Histoire Naturelle in Geneva and are listed in table V.

Two years before, in 1857, the first part with 9 plates of the cone section of the Thesaurus Conchyliorum (Sowerby II, 1842-1887) had appeared, with 7 illustrations of cones of the *C. cedonulli* complex. They are summarized in table IV, together with «*C. caledonicus*», which was published in the second part in 1858. There is only a brief and summarizing treatment in the text without mentioning of Hwass' infraspecific taxa.

TRYON (1884, vol. 6: 28) synonymized «C. cedonulli Hwass» with «C. nebulosus Solander» (= C. regius Gmelin, 1791), and from that time the original name «C. cedonulli Linné, 1767» was no longer used and generally treated as nomen dubium; it was thought that the figure in Seba, the basis for LINNÉ'S description, shows a variety of the indopacific C. ammiralis.

CLENCH (1942) synonymized the taxa curassaviensis, trinitarius, martinicanus, caracanus and grenadensis with C. regius Gmelin and recognized dominicanus as a separate species with surinamensis as a junior synonym. His illustration (pl. 4, fig. 4) however shows C. mappa mappa, a specimen from Governor RAWSON, which perhaps comes from Tobago. CLENCH & BULLOCK (1970) replaced the name dominicanus by insularis Gmelin, 1791, following KOHN (1966).

In a catalogue of the Conidae described and/or illustrated by HWASS (in BRUGUIÈRE), LAMARCK, DELESSERT, KIENER and CHENU and present in the MHNG, MERMOD (1947) established the presence of the holotypes of *trinitarius, martinicanus, grenadensis* and *caracanus* and reported other specimens belonging to the *C. cedonulli* complex, which in literature had been identified with the various infraspecific taxa of HWASS or which MERMOD himself identified with these taxa. A critical examination of this additional material reveals that most of these post-HWASS identifications do not coincide with the illustrations of HWASS' infraspecific taxa in the «Tableau...» (LAMARCK, 1798) and must be considered erroneous. MERMOD's compilation is summarized in Table V, together with the present status of the specimens.

The next revision of HWASS' taxa followed by KOHN (1968). He considered them «conspecific with the prior *C. insularis* Gmelin, 1791». Although citing them as subspecies, he did not determine «whether they represent valid subspecies or forms of infrasubspecific rank» (KOHN 1968: 450). Subsequently HOLEMAN & KOHN (1970) synonymized *C. insularis* Gmelin, *C. dominicanus* Hwass in Bruguière and *C. aurantius* Hwass in Bruguière with *C. mappa* Lightfoot, 1786. Concerning *C. aurantius* these authors had followed VAN MOL, TURSCH & KEMPF (1967).

The first «modern» author mentioning the name *cedonulli* in connection with the caribbean species was Coomans (1964). In his list of Southern Caribbean Conus species he included «*Conus cedonulli?* Linné, Lamarck (= *dominicanus* Hwass)».

In the late sixties the shell collector G. NOWELL-USTICKE found cones on the caribbean island of St. Vincent, of which he was convinced that these could be nothing else but the true *C. cedonulli* Linné, 1767, because 2 of these specimens were almost identical with SEBA'S illustration, on which LINNÉ'S description is based. Still thinking LINNÉ'S name being unavailable, USTICKE gave these cones new names (USTICKE, 1968) (see synonymy).

After having studied SEBA'S illustration of *C. ammiralis cedonulli* Linné in comparison with USTICKE'S similar specimen from St. Vincent, DUNN (1971) finally confirmed that *C. cedonulli* Linné, 1767 is the oldest available name for the *C. cedonulli* group, and he restored this name to its rightful position. KOHN (1976) followed this, considering *mappa*,

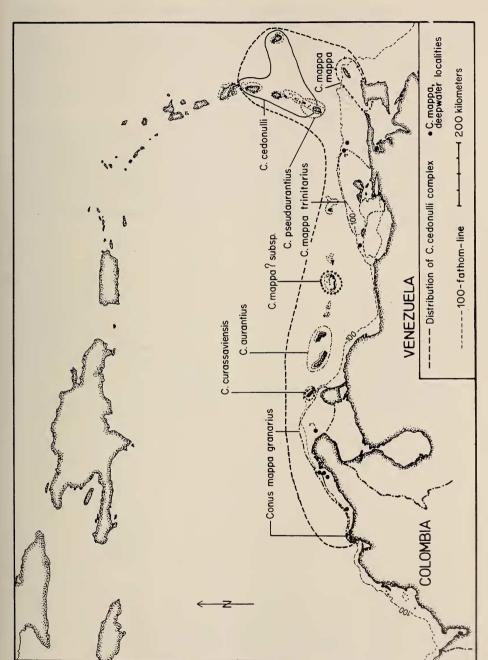


Fig. 1.

Distribution of the Conus cedonulli complex in the Caribbean (except C. scopulorum).

solidus and insularis junior synonyms of cedonulli; aurantius was recognized as provisionally valid, and HWASS' infraspecific taxa were provisionally regarded as of infrasubspecific rank.

As is evident from notes by SEAMON & SEAMON (1967) and VAN PEL (1969), field work began in the late sixties in the Netherlands Antilles, and, stimulated by this, during the last decade more fresh *C. cedonulli* material from several different localities and depths came to light. Zoogeographical and ecological aspects were taken into account by VINK (1977) in a first attempt to untangle the *C. cedonulli* complex. Relatively large lots of fresh material were compared and 5 taxa were tentatively regarded as of specific rank: *C. cedonulli* Linné, 1767, *C. aurantius* Hwass in Bruguière, 1792, *C. insularis* Gmelin, 1791, *C. mappa* Lightfoot, 1786 and *C. sanctaemarthae* Vink, 1977.

The present revision comprises the fossil *C. consobrinus* Sowerby I, 1850 and 11 recent taxa consisting of 7 species and 6 subspecies: *C. cedonulli* Linné, 1767 (with the subspecies *C. c. cedonulli*, *C. c. insularis* Gmelin, 1791, *C. c. dominicanus* Hwass in Bruguière, 1792), *C. pseudaurantius* n. sp., *C. aurantius* Hwass in Bruguière, 1792, *C. mappa* Lightfoot, 1786 (with the subspecies *C. m. mappa*, *C. m. trinitarius* Hwass in Bruguière, 1792, *C. m. granarius* Kiener, 1848), *C. curassaviensis* Hwass in Bruguière, 1792, *C. archon* Broderip, 1833 and *C. scopulorum* van Mol, Tursch & Kempf, 1971. *C. archon* lives in the Eastern Pacific, the remaining species in the Western Atlantic.

# TABLE I HWASS' taxa of cones of the Conus cedonulli complex

Correct locus typicus	St. Vincent, Lesser Antilles	Trinidad	Aruba, Netherlands Antilles	Islas Los Testigos, Venezuela	(this form from SW-shore of St. Lucia)
Present status	C. cedonulli cedonulli Linné, 1767 valid species	C. mappa mappa Lightfoot, 1786 valid species	C. curassaviensis Hwass in Bruguière, 1792 valid species	C. mappa trinitarius Hwass in Bruguière, 1792 valid subspecies	C. cedonulli cedonulli Linné, 1767 variety
Whereabouts of type, type No. and locus typicus cited by Hwass	Type missing Mers de l'Amérique méridionale	Type missing Les mêmes mers que le véritable cédonulli	Type missing Côtes de l'isle de Curaçao	MHNG 1106/59 (holotype) Océan américain et c'est de l'isle de la Trinité qu'on l'apporte ordinairement	MHNG 1106/60 (holotype) Côtes de l'isle de la Dominique
Fig. in Tableau	pl. 316, fig. 1	pl. 316,	pl. 316,	pl. 316, fig. 2	pl. 316,
Hwass' taxon with references cited by Hwass	C. cedonulli amiralis References cited: Klein Seba Martini D'Argenville Favanne Regenfuss Schröter	C. cedonulli mappa References cited: KNORR MARTINI FAVANNE	C. cedonulli curassavicnsis References cited: D'Argenville Seba Regenfuss Favanne	C. cedonulli trinitarius References citcd: FAVANNE	C. cedonulli martinicanus References cited: KNORR

Hwass' taxon with references cited by Hwass	Fig. in Tableau	Whereabouts of type, type No. and locus typicus cited by Hwass	Present status	Correct locus typicus
C. cedonulli dominicanus References cited: Martini	pl. 316, fig. 8	Type missing Côtes de l'isle de la Dominique dans l'Océan américain	C. cedonulli dominicanus Hwass in Bruguière, 1792 valid subspecies	Mustique, Grenadines
C. cedonulli surinamensis References cited: Martini Favanne	pl. 316, fig. 9	Type missing Surinam, parce qu'on la pêche dans cette partie de l'Amérique	C. mappa trinitarius Hwass in Bruguière, 1792	Islas Los Testigos, Venezuela
C. cedonulli grenadensis	pl. 316, fig. 5	MHNG 1106/58 (holotype) Grenada, de l'isle de ce nom, l'une des Antilles d'où on l'apporte	C. cedonulli cedonulli Linné, 1767	St. Vincent
C. cedonulli caracanus References cited: None	pl. 316, fig. 6	MHNG 1106/57 (holotype) Côte de Caracas, dans l'Amérique méridionale au nord de la Guyane	C. cedonulli ?insularis Gmelin, 1791	St. Lucia
C. aurantius References cited: LISTER KNORR KLEIN FAVANNE GUALTERI MARTINI SEBA	pl. 317,	MHNG 1106/42 (lectotype) Océan asiatique et se trouve plus particulièrement qu'ailleurs, aux isles Philippines	C. <i>aurantius</i> Hwass in Bruguière, 1792 valid species	Curação (locality designated by CLENCH & BULLOCK (1970))
C. caledonicus References cited: None	pl. 321, fig. 10	Côtes de la Nouvelle Calédonie	C. cedonulli cedonulli Linné, 1767, dark unicoloured variety	St. Vincent (locality designated by Coomans et al. (1983))

### TABLE II

(References without figures in Vol. 12 of 1st ed. (SCHUBERT & WAGNER) to figures in Vols. 2 (MARTINI) and 10 (CHEMNITZ) are not cited) The Conus cedonulli complex in the first and second edition of MARTINI/CHEMNITZ, Systematisches Conchylien-Cabinet

					1		
Present status of figured specimen	C. cedonulli cedonulli L.	C. aurantius Hw. in Brug.	C, aurantius Hw. in Brug.	C. cedonulli insularis Gmelin	Most probably C. cedonulli cedonulli L.	C. mappa mappa Lightfoot	C. cedonulli cedonulli L.
Remarks	Plates in both editions in same composition	Plates in both cditions partly in same composition	Plates in both editions partly in same eomposition	Figure representative of holotype of C. insularis Gmel., selected by Kohn	Plates in both editions in same composition	Holotype of C. solidus Gmel., figured, specimen in ZMC	Plates in both editions in same composition Holotype of C. caledonicus, Hw. figured, specimen in MHNG
Name and locality in K0sTER	C. cedo nulli Klein (text), C. cedo nulli Chemitz (tegend),,,,Meer and den Antillen und der östliehen Küste Südamerikas"	C. auranius Hwass (text and legend) ,,im asiatischen Ozean, an den Philippinen"	Var. C. C. cedo nulli curassaviensis (text) C. auranius Hwass (legend) "an den Küsten der Insel Curassao"	Var. H.C. cedo nulli grenadensis (text) C. cedo nulli Ch. (legend) an den Küsten der Insel Grenada, eine der Kleinen Antillen".	Var. F. C. cedo nulli dominicanus (text) C. cedo nulli Hwass (legend) "bei der Insel Dominica"	Var. G. C. cedo nulli surinamensis (text) (no legend) "an der Küste von Surinam"	C. caledonicus Hwass (text and legend) "Bei Cooks Weltumseglung im stillen Meer an den Küsten von Neu-Caledonien entdeckt"
Treatment and fig. in 2nd ed.	KOSTER: 18, 14-19; pl. 17, fig. 3 Wenkaupe, 1873: 141	Küster: 104-105; pl. 20, fig. 6 Weinkauff: 175	Kuster: 16-17; pl. 18, fig. 1	Кохпек. 19; pl. 18, fig. 2	Kuster: 18; pl. 4, fig. 1	Kuster. 18; pl. 4, fig. 8	Kosner. 12; pl. 2, fig. 1
Taxa eited in 1st. ed. and/or in GMELIN (partly after RICHARDSON & al., 1979)	Amiralis Cedo nulli Linné: Chenvitz II (Martin): 274 C. ammiralis cedo nulli: Gmelli: 3380	C. varius Linné, 1758: CHEMNITZ II (MARTINI): 325 C. varius: GMELIN: 3385	C. varius; GMELN: 3385	C, insularis; Gmelin: 3389	C, ammiralis cedonulli var. : GMELIN: 3380	C. solidus: Gmelin: 3389	C. caledonicus Hwass: Chemnitz XII (Schubert & Wagner): 29
Treatment and fig. in 1st. ed (with german names)	MARTINI, 1773, vol. 2: 273-274 pl. 57, fig. 633 ,,der Cedo nulli",,Die Unvergleichliche"	Vol. 2: 324-325; pl. 61, fig. 679 "die gekörnte Landchartentute" "der Bastard Cedonulli"	Vol. 2: 325-326; pl. 62, fig. 682 "die glattgewundene Landchartentute"	Vol. 2: 327; pl. 62, fig. 683 "Admiral der Eylandstute"	Снеммитz, 1788 Vol. 10: 47-50; pl. 141, fig. 1306 "Königin der Südsee"	Vol. 10: 59 pl. 141, fig. 1310 "der dickschaliehte Kegel"	SCHUBERT & WAGNER, 1829, Vol. 12: 29-30; pl. 220, fig. 3050 ,,,der kaledonische Kegel"

Present status of figured specimen	Probably C. mappa mappa Lightfoot	C. cedonulli ?insularis Gmelin	C. cedonulli cedonulli L.	C. mappa trinitarius Hw. in Brug.	C. cedonulli cedonulli L.
Remarks		Holotype of C. cedonulli caracanus Hw. figured, specimen in MHNG	Holotype of C. cedo nulli ammiralis Hw. figured, specimen missing	Refers to FAVANNE, BRUGUIÈRE and Tableau Encycl. (in both ed.)	Refers to Knorr, BRUGUIÈRE and Tableau Encycl. (in both ed.)
Name and locality in KUSTER	Var. B. C. cedo nulli Mappa (text) C. cedo nulli Hwass (legend) "in den südamerikanischen Meeren"	Var. I. C. cedo nulli caracanus (text) C. cedo nulli Hwass (text) (text)an den Küsten von Caracas"	Var. A C. cedo nulli Anmiralis (text) C. cedo nulli Hwass (legend) "in den südamerikanischen Meeren."	Var. D. C. cedo nulli trinitarius "bei der Insel Trinitat"	Var. E. C. cedo nulli marinicanuswahrscheinlich auch bei Martinic, da sie daher den Namen hat"
Treatment and fig. in 2nd ed.	KÜSTER: 16; pl. 2, fig. 4	Koster. 19; pl. 2, fig. 5	Kuster, 15-16; pl. 2, fig. 6	Küster: 17; (no figure)	Küster: 17-18; (no figure)
Taxa cited in 1st. ed. and/or in GMELIN (party after RICHARDSON & al., 1979)	C. cedo nulli mappa Bruguière: CHEMNITZ XII (SCH. & W.): 35	C. cedo nulli caracanus Briguière: CHEMNITZXII (SCH. & W.): 35	C. cedo nulli Ammiralis Bruguière: CHENNIZ XII (SCH. & W.): 33	C. cedo nulli trinitarius Bruguière: CHEMNIZ XII (SCH. & W.): 34	C. cedo nulli martinicanus Bruguière: CHENNITZ XII (SCH. & W.): 34
Treatment and fig. in 1st. ed (with german names)	Vol. 12: 33, 36; pl. 220, fig. 3053 ,,der Landkarten- Cedonulli"	Vol. 12: 35, 38; pl. 220, fig. 3054	Vol. 12: 32-33; 35-36; pl. 220, fig. 3055 ,,der ächte Cedonulli"	Vol. 12: 34; 36-37; (no figure)	Vol. 12: 34; 37; (no figure)

TABLE III

REEVE'S varieties of *Conus cedonulli* (Conch, Icon., CONUS, pl. 9, spec. 46)

Reeve's varieties	Whereabouts of figured specimen	Present status
Variety a (coll. Cuming)	BM(NH) 1969342	C. curassaviensis Hwass in Bruguière, 1792
Variety b (coll. STAINFORTH)*	?	C. cedonulli cedonulli Linné, 1767
Variety c (coll. STAINFORTH)	?	Probably <i>C. curassaviensis</i> Hwass in Bruguière, 1792
Variety d (coll. STAINFORTH)	BM(NH) 1969343	C. cedonulli cedonulli Linné, 1767
Variety e (coll. STAINFORTH)	?	C. cedonulli cedonulli Linné, 1767
Variety f (coll. STAINFORTH)	?	C. cedonulli cedonulli Linné, 1767
Variety g (coll. Stainforth)	?	C. cedonulli Linné, 1767 black form

<sup>\*</sup>According to Dance (1966) some types of the Stainforth collection are in the National Museum of Wales, Cardiff, but on a visit there, Reeve's varieties of *C. cedonulli* could not be traced.

 $\label{total constraints} Table~IV$  The  $\it Conus~cedonulli~complex~in~Sowerby's~Thesaurus~Conchyliorum$ 

Figure in Thesaurus	Name and locality in Thesaurus	Present status	Remarks
pl. 189 [Conus 3], fig. 35 pl. 189 [Conus 3], fig. 36	C. leucostictus Gmelin* Philippines, Moluccas	C. aurantius Hwass in Bruguière, 1892 C. aurantius Hwass in Bruguière, 1792 black form	
pl. 190 [Conus 4], fig. 64		C. cedonulli cedonulli Linné, 1767 black form	Same specimen as "var g" of Reeve
pl. 190 [Conus 4], fig. 65 pl. 190 [Conus 4], fig. 66	C. cedonulli Brug. West Indies	C. cedonulli cedonulli L. C. curassaviensis Hwass in Bruguière, 1792	Probably same specimen as "var a" of Reeve (specimen BM(NH) 1969343)
pl. 190 [Conus 4], fig. 67		C. cedonulli cedonulli L.	Probably same specimen as "var d" of Reeve (specimen BM(NH) 1969343)
pl. 190 [Conus 4], fig. 68		C. cedonulli insularis Gmelin	
pl. 203 [Conus 17], fig. 413	C. caledonicus Brug.	C. cedonulli cedonulli L. dark unicolor form	"Copied", most probably from Tableau Encycl.

<sup>\*</sup>C. leucostictus Gmelin, 1791 is a junior synonym of C. regius Gmelin, 1791 (see KOHN, 1966: 89).

# TABLE V

MERMOD'S identification of cones of the C. cedonulli complex in the MHNG, based on HwASS taxa

	cimen(s) in MHNG Specimen illustrated in: and remarks	HNG 1104/91 FAVANNE, Pl. 16, fig. D5 Conus cedonulli cedonulli Cheser, pl. 40, fig. 2 St. Vincent Chenu I, fig. 1445* (faded colours)	ING 1104/88  Delessert, pl. 40, fig. 6  C. cedonulli cedonulli L.  St. Vincent  St. Vincent  (faded colours)	ING 1104/92  C. cedonulli insularis  G. cedonulli insularis	Holotype MHNG 1106/59 Tableau pl. 316, fig. 2 C. mappa trinitarius 40.0 x 21.5 mm DELESSERT, pl. 40, fig. 8 Hwass in Bruguière, 1792 CHEVU I, COMDS pl. 4, fig. 8 Islas Los Testigos CHENU II, fig. 1450, 1451 KENER, pl. 16, fig. 1e	Holotype MHNG 1106/60 Tableau pl. 316, fig. 3 C. cedonulli cedonulli L. DELESSERT, pl. 40, fig. 9 St. Lucia CHENU I, Conus pl. 4, fig. 9 CHENU II, fig. 1455 KIENER, pl. 16, fig. 1d	ING 1104/90 C. cedonulli cedonulli L. St. Vincent from coll HwAss (worn specimen, faded colours)	ING 1104/89  Delessert, pl. 40, fig. 4  C. cedonulli dominicanus CHENU I, Conus pl. 4, fig. 4  Hwass in Bruguière Grenadines, probably Mustique	NG 1104/87
	Specimen(s) in MHNG	MHNG 1104/91 50.0 x 26.5 mm coll. Lamarck	MHNG 1104/88 45.2 x 27.5 mm coll. Lamarck	MHNG 1104/92 47.0 x 23.5 mm coll. Hwass or Sollier ex. coll. Lamarck?	Holotype MHNG 1106, 40.0 x 21.5 mm coll. Hwass	Holotype MHNG 1106, 41.5 x 21.5 mm coll. Hwass	MHNG 1104/90 41.0 x 23.0 mm not from coll HwASS	MHNG 1104/89 49.0 x 25.0 mm coll. HwAss	MHNG 1104/87
Toyon of Huvee	cited by Mermod	C. cedonulli amiralis	C. cedonulli mappa	C. cedonulli curassaviensis	C. cedonulli trinitarius	C. cedonulli marinicanus	C, cedonulli dominicanus	C. cedonulli surinamensis	

Present status with presumable locality and remarks	C. cedonulli cedonulli L. St. Vincent (faded colours)	C. cedonulli insularis Gmelin ?St. Lucia (black form)	C. cedonulli L. ?St. Vincent (black form)	C. mappa trinitarius Hwass in Bruguière, 1792, light greyish form Eastern Venezuela or Los Testigos	C. cedonulli insularis Gmelin, 1791 St. Lucia (slightly worn specimen)
Specimen illustrated in:	Tableau, pl. 316, fig. 5 Delesser, pl. 40, fig. 3 Chenu I, Comus pl. 4, fig. 3 Chenu II, fig. 1454	Tableau, pl. 316, fig. 6 DELESSER, pl. 40, fig. 5 CHENU I, Conus pl. 4, fig. 5 CHENU II, fig. 1456 SCH. & W., pl. 220, fig. 3054 KÜSTER, pl. 2, fig. 2	DELESSERT, pl. 40, fig. 7 CHENU I, Conus pl. 4, fig. 7 CHENU II, fig. 1446, 1447 KIENER, pl. 16, fig. 1b		Снеии II, fig. 1520, 1521
Specimen(s) in MHNG	Holotype MHNG 1106/58 46.5 x 23.2 mm coll. Hwass	Holotype MHNG 1106/57 47.0 x 25.5 mm coll. Hwass	MHNG 1104/93 52.2 x 28.0 mm coll. Hwass or coll. Sollier?	MHNG 1104/95 42.5 x 22.0 mm coll. Lamarck?	MHNG 1104/94 40.0 x 23.5 mm coll. Lamarck?
Taxon of Hwass. cited by Mermod	C. cedonulli granadensis [sic.!]	C. cedonulli caracanus ,			

\*legend in CHENU: "C. mappa"

CHENU, III. Conchyl. (1843-1853), Conus pl. 4: 1847, fide SHERBORN & SMITH, 1911

CHENU, Man. Conchyl. (1859)

DELESSERT:

CHENU II: FAVANNE:

CHENU I:

FAVANNE & FAVANNE, 3rd. ed of d'Argenville's La Conchyliologie (1780) DELESSERT, Recueil... (1841)

KUSTER & WEINKAUFF. CONCH. Cab., 2. ed. CONUS (1837-1873) SCHUBERT & WAGNER, CONCH. Cab., 1. ed., Vol. 12 (1829) Kiener, Species Général... (1845-1850) SCH. & W.: KIENER: KÜSTER:

#### IL SYSTEMATICS AND TAXONOMY

#### I) Conus cedonulli Linné, 1767

- 1767 Conus Ammiralis cedo nulli Linné, Syst. Nat. ed. 12: 1167
- 1792 C. cedonulli amiralis Hwass in Bruguière, Encycl. meth. 1: 602; Tableau: pl. 316, fig. 1
- 1792 C. cedonulli martinicanus Hwass in Bruguière, Encycl. meth., 1: 603; Tableau: pl. 316, fig. 3 (holotype MHNG 1106/60)
- 1792 C. cedonulli grenadensis Hwass in Bruguière, Encycl. meth. 1: 603; Tableau: pl. 316, fig. 5 (holotype MHNG 1106/58)
- 1792 C. caledonicus Hwass in Bruguière, Encycl. meth. 1: 634; Tableau: pl. 321, fig. 10 (holotype MHNG 1106/73)
- 1843 C. cedonulli Klein-REEVE, Conch. Icon. Conus, pl. 9, sp. (fig.) 46, var. b, d, e, f, g
- 1857 C. cedonulli Brug.-Sowerby II, Thesaurus Conchyliorum, 3, Conus: 7; pl. 180 [Conus pl. 4], fig. 64, 65, 67
- 1968 C. holemani Usticke, Carib. Cones...: 19; pl. 3, No. 1011
- 1968 C. nulli-secundus Usticke, Carib. Cones...: 20-21; pl. 3, No. 1010
- 1970 C. mappa Lightfoot-Holeman & Kohn, J. Conch. 27: 135-136 [partim]; pl. 5, fig. 5 (non Lightfoot, 1786)
- 1971 C. cedonulli Linné-Dunn, Veliger 13 (3): 290; pl. 6, fig. 1
- 1976 C. cedonulli Linné-KAICHER, Card Catal., Pack 11: 1108
- 1977 C. cedonulli Linné-LOZET, Shells Carib.: 98, fig. 161
- 1977 C. cedonulli Linné-Vink, Zool. Meded. 51: 86, 88; pl. 1, fig. 1; pl. 2, fig. 1-2
- 1977 C. cedonulli grenadensis Hwass-Kaicher, Card Catal., Pack 14: 1426 (holotype ill.)
- 1977 C. cedonulli martinicanus Hwass-KAICHER, Card Catal., Pack 14: 1429 (holotype ill.)
- 1979 C. cedonulli Linné-Walls, Cone sh.: 200 (operculum shown on upper left figure is not from cedonulli)
- 1982 C. cedonulli Linné-Coomans, Moolenbeek & Wils, Basteria 46: 54; fig. 188
- 1983 C. cedonulli Linné-Coomans et al., Basteria 47: 102-103 [partim]; fig. 375-380
- 1983 C. cedonulli forma caledonicus Hw.-Coomans et al., Basteria 47: 137; fig. 379-380

T y p e: Specimen figured by SEBA (1759: pl. 4, fig. 8) designated by KOHN (1976) as representative of lectotype. This specimen, also figured by KNORR (1772, vol. 6: pl. 1, fig. 1) is the only representative and hence holotype (COOMANS *et al.* 1983). Figured specimen missing, apparently lost (DUNN 1971) or supposed to be "kept in some European collection" (COOMANS *et al.* 1983: 102, see there for details).

Locus typicus: "O. Americae meridionalis", here restricted to St. Vincent, Lesser Antilles, Caribbean Sea.

Description: Mean shell length 47.1 mm (S.D. = 6.8 mm, Range: 31.8-61.5 mm, N = 50; morphometry see table VIII). Spire moderately elevated, in adult specimens concave-sided. Whorls canaliculate, early whorls coronated, shoulder of body whorl smooth. Outline of body whorl from almost straight to very slightly convex with greatest width just somewhat below the shoulder. Protoconch elevated, following teleoconch whorls in the first instance with the same steep slope, which gradually weakens towards the body whorl. Surface with beaded spiral threads, well developed on the lower third, becoming weaker or obsolete towards the shoulder. Larger part of shell smooth, in some specimens of the typical form the shades of the markings make it seem granulated (DANCE 1966: 234). No internal restriction on the anterior third of the columella within the aperture (see *C. mappa*). Colour quite variable, shells brown or black with white maculations or white with brown or black maculations covering large areas or only consisting of medium-

sized to small patches. Besides this pattern spiral lines of white and brown dots. Dots in the brown areas occasionally outlined with dark brown and interconnected by dark brown spiral threads.

H a b i t a t: Sand or coral rubble bottom with some vegetation, from 2 to 50 m, but also dredged from 160 m.

Distribution: Lesser Antilles from Grenada to St. Lucia and off Barbados.

Discussion: Adult specimens of *C. cedonulli* are easily distinguished from *C. aurantius* by the smooth shoulder of the body whorl, the more stout appearance and the form of protoconch and first teleoconch whorls. *C. curassaviensis* is smaller than *C. cedonulli*, with more convex sides of the body whorl, a relatively higher, slightly concave spire and sometimes a slightly more rounded shoulder. *C. mappa* is somewhat similar in outline to *C. cedonulli*, although usually it has a higher, more stepped and often less concave spire. In some specimens of *C. cedonulli* the shoulder is slightly more rounded than in *C. mappa*. Distinction between *C. cedonulli* and *C. mappa* can best be made on basis of presence or absence of an internal restriction on the columella within the aperture (see *C. mappa*).

C. cedonulli is confined to oceanic islands and not found on the continental shelf. It has developed 3 subspecies with constant differences in colour and pattern. Deep water specimens of C. cedonulli insularis have a lighter, slightly more slender shell. Within each subspecies several colour varieties can be distinguished.

#### 1) Conus cedonulli cedonulli Linné, 1767 (pl. 1, fig. 1-13; pl. 2, fig. 1-9; pl. 3, fig. 1-3)

S p e c i m e n s e x a m i n e d: St. Lucia: Anse la Raye and Castries, various subrecent shells (pl. 1, fig. 9). St. Vincent: Kingstown Harbour, various subrecent shells from dredge spoil (pl. 1, fig. 6, 12); various specimens or fresh shells from the leeward side and near Young's Island. (pl. 2, fig. 6)

H a b i t a t: On mineral (often black volcanic) or coral sand bottom with some vegetation, from 2 to about  $50\ m.$ 

Distribution: Lesser Antilles. Endemic to the W-coast of St. Lucia and St. Vincent.

D is c ussion: Typical C. cedonulli cedonulli shells are orange brown to mahogany brown with numerous irregular purplish white patches mainly at and below midbody. Body whorl with 26-30 spiral lines of white and brown dots in the whitish areas and of purplish white circles in the dark areas. These are outlined with dark brown and interconnected by spiral threads of dark brown. Some of the purplish white circles or small flecks on the upper half are larger at regular intervals, forming small patches comparable to those on the mid-region and below. Shoulder and spire also with purplish white patches. Pattern very variable, with sometimes purplish white areas coalescing into 1-2 irregular spiral bands ("C. cedonulli martinicanus Hwass in Bruguière", pl. 1, fig. 7-9) or forming zigzag or V-shaped markings (pl. 2, fig. 5; 7). In very few specimens whitish markings totally absent, colour then uniform mahogany with dark brown spiral lines ("C. caledonicus Hwass in Bruguière", pl. 3, fig. 1-3). Colour of the dark areas also very variable: from mahogany to reddish like burgundy wine or more olive-green. About 10% of the specimens in a nor-

mal C. cedonulli cedonulli population are pitch black with whitish markings as described above (pl. 2, fig. 4-5). When faded in beach-worn or subrecent specimens the mahogany turns to bright yellow orange, the black to reddish brown without darker outlining ("C. holemani Usticke").

Before the recent discovery of live specimens the true colours of *C. cedonulli cedonulli* were not known, and descriptions in the 18th and 19th century were mainly based on subrecent specimens usually found on the beach or in the spoil of dredgings. Until recently *C. caledonicus* was not recognized as a colour form of *C. c. cedonulli* (see HUNT 1980 and COOMANS *et al.* 1983). Evidence that the black specimens are also colour varieties was found in one specimen with mahogany brown shell, which continued to produce a black shell after damage had occurred to the lip. The "form" *martinicanus* with a continuous subcentral whitish band is more commonly found on the W-shore of St. Lucia. The pattern of the holotype of *C. cedonulli grenadensis* Hwass in Bruguière (MHNG 1106/58, pl. 1, fig. 10-11) with dark tongues or bulges invading the light coloured mid-area somewhat resembles that of some specimens of *C. pseudaurantius* n. sp. from Grenada, but the latter is clearly distinguished by its shape. A cone similar to specimen MHNG 1106/58 has been dredged from Kingstown Harbour, St. Vincent (pl. 1, fig. 12).

#### 2) Conus cedonulli insularis Gmelin, 1791 (pl. 3, fig. 4-11, pl. 4, fig. 13-14)

- 1791 Conus insularis Gmelin, Syst. Nat., ed. 13: 3389
- 1792 C. cedonulli caracanus Hwass in Bruguière, Encycl. meth. 1: 603; Tableau: pl. 316, fig. 6 (holotype MHNG 1106/57)
- 1859 C. curassaviensis Lamarck-Chenu, Man. Conch.: 243, fig. 1453c (non Hwass in Bruguière, 1792)
- 1966 C. insularis Gmelin-Kohn, J. Linn. Soc. Lond. (Zool.) 46 (308): 86; pl. 2, fig. 4
- 1968 C. dominicanus Hwass-STIX & ABBOT, The Shell, pl. 130 (specimen probably from Barbados)
- 1977 C. dominicanus Hwass-Lozet, Shells Caribbean: 98, fig. 160a (middle row, first and fourth specimen) (non Hwass in Bruguière, 1792)
- 1977 C. cedonulli Linné-VINK, Zool. Meded. 51: pl. 2, fig. 3
- 1977 C. cedonulli caracanus Hwass-KAICHER, Card Catal., Pack 14: 1427 (holotype ill.)
- 1983 C. cedonulli ssp./forma caracanus Hwass-Coomans, Moolenbeek & Wils, Basteria 47: 86; fig. 382

T y p e: Specimen figured by MARTINI (1773), vol. 2, pl. 62, fig. 683 (coll. J. F. BOLTEN) designated by KOHN (1966) as representative of holotype (pl. 3, fig. 4). Whereabouts of specimen unknown.

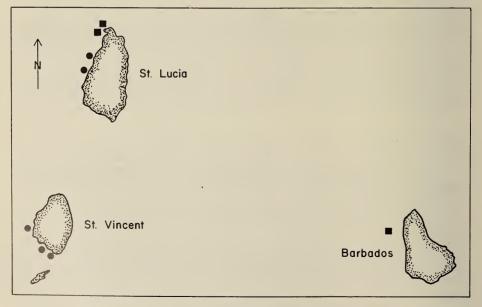
Locus typicus: Not given, here selected Gros Islet Bay, St. Lucia, Lesser Antilles.

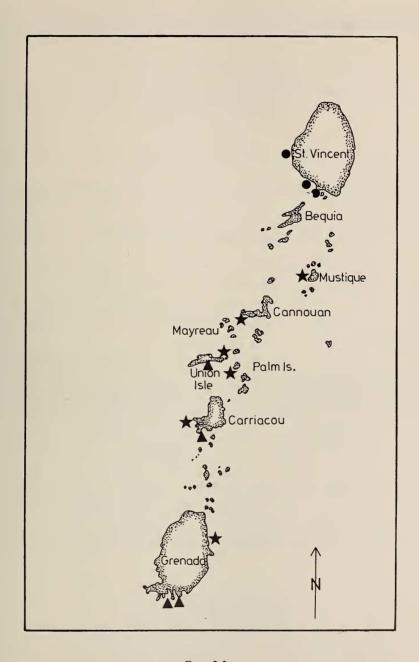
S p e c i m e n s e x a m i n e d: St. Lucia: North coast, 20 m, 1 specimen; Gros Islet Bay, various shells from dredge spoil and from the beach, mostly subrecent with faded colours. Barbados: 2 specimens (pl. 3, fig. 9-11) and a few shells dredged off St. James in about 160 m.

H a b i t a t: Sand and rubble bottom from about 20 m (St. Lucia) to 160 m.

Distribution: Yet only known from St. Lucia (N-shore) and Barbados, Lesser Antilles.

Discussion: Conus cedonulli insularis differs from C. c. cedonulli in having the mahogany brown background more or less broken up to isolated irregular brown to yellow brown patches or maculations arranged in 2 spiral rows on a whitish, yellowish or pinkish background, the patches in the lower row sometimes coalescing into a spiral band. Fine spiral lines as in C. c. cedonulli. Most known shells from St. Lucia are subrecent, in these the patches vary from pale yellow with darker outline to reddish brown without outline. These reddish brown patches must have been black in fresh specimens, like in C. c. cedonulli. The holotype of C. cedonulli caracanus Hwass in Bruguière, 1792 (pl. 4, fig. 14) seems to be such a specimen, it can best be compared with the subrecent specimen on pl. 3, fig. 5. But as there remains an uncertainty, especially also concerning the other specimen of C, c, caracanus (pl. 4, fig. 15) with larger dark markings and convex-sided body whorl, as there are no localities, and as fresh black specimens have not yet been seen, C. c. caracanus has been put into the synonymy of C. c. insularis only provisionally. Nevertheless, the absence of an internal restriction (see C. mappa) proves that it is C. cedonulli, COOMANS et al. (1983: 86) cite shells of the C. cedonulli complex from Aruba identical to the holotype of C. c. caracanus, but they admit that also specimens from Grenada show an identical pattern. However, the specimens from Aruba here identified with C. curassaviensis are more slender and the spiral lines of white and brown dots and dashes generally are placed closer together than in the holotype of C. c. caracanus. — The specimen figured as "C. curassaviensis" by CHENU (1859) is specimen MHNG 1104/92, a typical C. c. insularis (pl. 3, fig. 7). VINK (1977) erroneously identified the type figure of C. insularis (MAR-TINI 1773, pl. 62, fig. 683) with specimens of C. curassaviensis from Aruba. The Aruban specimens have a less triangular shape and more dense dotted spiral lines. — Subrecent shells of intergrades between C. c. cedonulli and C. c. insularis have been found along the





Figs. 2-3.

Distribution of Conus cedonulli and C. pseudaurantius in the Lesser Antilles

• C. cedonulli cedonulli ■ C. c. insularis ★ C. c. dominicanus ▲ C. pseudaurantius

west coast of St. Lucia. The few known Barbados specimens (pl. 3, fig. 9-11) are quite similar to the St. Lucia shells, but have slightly larger orange brown patches and are more slender.

#### 3) Conus cedonulli dominicanus Hwass in Bruguière, 1792 (pl. 4, fig. 1-7)

- 1792 Conus cedonulli dominicanus Hwass in Bruguière, Encycl. meth. 1: 603; Tableau: pl. 316, fig. 8.
- 1977 C. dominicanus Hwass-Lozet, Shells Caribbean: 96, fig. 160b (specimen apparently from Mustique)

T y p e: Holotype probably lost. Type figure in LAMARCK (1798, Tableau) here reproduced (pl. 4, fig. 1).

Locus typicus: "sur les côtes de l'isle de la Dominique dans l'Océan Américain", here corrected to Mustique, Grenadines, Lesser Antilles.

S p e c i m e n s e x a m i n e d: Various specimens or fresh shells from Cannouan, Mustique (pl. 4, fig. 3), Union Isle (pl. 4, fig. 4), Palm Island (pl. 4, fig. 5), the SW-shore of Carriacou (pl. 4, fig. 6-7) and the NE-coast of Grenada.

H a b i t a t: On sand or coral sand bottom, partly with sea grass, from 2 to 20 m.

 $D\ i\ s\ t\ r\ i\ b\ u\ t\ i\ o\ n$  : Islands of the Grenadines from Bequia to Carriacou; Grenada (NE-coast).

D i s c u s s i o n: The population of *C. cedonulli dominicanus* is separated by the Bequia Channel from *C. c. cedonulli* of St. Vincent. In general appearance the shells of *C. c. dominicanus* seem to look "heavier", but there are no significant differences in shell shape. Spire concave-sided as in *C. c. cedonulli* ("Sa spire est légèrement comprimée sur les côtes comme celle du cédonulli amiral", Hwass i. Br., 1792). Colour bluish white with numerous small orange-brown to reddish brown patches or axial flames, mainly arranged in 2 bands, a narrower one near the base and a broader one on the upper part of the body whorl. Sometimes the lower part of the upper broad band is nearly or completely separated, forming a narrow third band of smaller patches at midbody (e.g. pl. 4, fig. 6). Axial flames of upper band often coalescing. Body whorl covered with slightly granulated close set spiral lines consisting of brown and white dots in the dark areas and of brown dots in the white areas. Contrary to *C. c. cedonulli* and *C. c. insularis* the brownish and white areas and dots are not outlined by dark brown. There are minor differences between the populations on the different islands within the Grenadines. The Carriacou specimens are slightly smaller.

#### II) Conus pseudaurantius n. sp. (pl. 4, fig. 8-12, pl. 6, fig. 1-5)

- 1968 Conus dominicanus Hwass-USTICKE, Carib. Cones...: 19, pl. 3, No. 1009 (non Hwass in Bruguière, 1792)
- 1977 C. dominicanus Hwass-Lozet, Shells Caribbean: 98, fig. 160 (middle row, second and third specimen) (non Hwass in Bruguière, 1792)
- 1977 C. aurantius Hwass-Vink, Zool. Meded. 51: 88 [partim], pl. 4, fig. 3

D i a g n o s i s: A comparatively small, slender cone of the *Conus cedonulli* complex with a rather short spire in relation to height of the body whorl, knobbed shoulder and slightly convex body whorl.

T y p e s: Muséum d'Histoire Naturelle, Geneva: Holotype MHNG 983/991,  $34.5 \times 17.4$  mm (pl. 6, fig. 1), Paratype MHNG 975/428,  $33.0 \times 16.5$  mm (pl. 6, fig. 4); Muséum National d'Histoire Naturelle Paris: 1 paratype  $32.8 \times 16.8$  mm (pl. 4, fig. 9); National Museum of Natural History, Washington: 1 paratype USNM 842110,  $28.6 \times 15.4$  mm; coll. v. Cosel: 1 paratype  $29.9 \times 14.2$  mm (pl. 6, fig. 3); coll. Vink: 6 paratypes (max. size  $41.0 \times 19.0$  mm, pl. 6, fig. 5).

Locus typicus: Union Isle, Lesser Antilles, Caribbean Sea.

Description: Mean shell length 34.5 mm (S.D. = 3.7 mm, Range: 29.9-41.0 mm, N = 12). Shell quite slender (mean relative diameter 0.62; morphometry see table IX), with short to moderately elevated, rather straight-sided spire. Outline of body whorl slightly convex, its surface with weak spiral rows of granules, becoming obsolete towards the posterior half of the worl. Shoulder of the body whorl and spire worls tuberculated with numerous knobs. In some fully adult specimens knobs on the last half of the body whorl becoming obsolete. Aperture broadening anteriorly producing a rounded base. No internal restriction on the anterior third of the columella within the aperture (see *C. mappa*). Colour pattern consisting of 2 irregular orange brown, red brown or black spiral bands of irregular isolated or interconnected patches. Background colour yellowish white, purplish white or pure white. On the body whorl numerous spiral lines of dark brown dots in the light areas and very small close-set white dots in the dark areas. Inside of aperture white with a brownish rim along the margin. In young specimens pattern of the outside showing through.

S p e c i m e n s e x a m i n e d: Grenada: various specimens from Calivigny Island near the S-coast (pl. 4, fig. 9-10) and subrecent shells from dredgings near Westerhall Bay (Ft. Jeudy Bay) (pl. 4, fig. 11-12). Carriacou: 1 specimen from the S-coast (pl. 4, fig. 8). Union Isle: 4 specimens (pl. 6, fig. 1-3; 5).

Habitat: On sand or coral rubble in shallow water (3-5 m).

D i s t r i b u t i o n : Southernmost part of Lesser Antilles from Union Isle to Grenada.

Derivatio nominis: The name pseudaurantius indicates the general similarity of the new species to C. aurantius Hwass in Brug.

D i s c u s s i o n: Within the *C. cedonulli* complex, *C. pseudaurantius* is most similar to *C. aurantius* and was erroneously identified with that species by VINK (1977). However, it is distinguished by its smaller size, the more rounded base, smaller and less articulate shoulder knobs and a shorter spire in relation to the height of the body whorl. In *C. aurantius* the spiral rows of small dots are more dense and the dots more numerous than in *C. pseudaurantius*. The geographic ranges of *C. aurantius* and *C. pseudaurantius* are separated by a distance of 700 km. From *C. cedonulli*, the new species differs mainly by the knobbed shoulder of the body whorld, the more slender outline, the smaller size and the somewhat more equally convex-sided body whorl. *C. curassaviensis* is larger, broader and heavier and has a smooth body whorl shoulder; *C. mappa* is well distinguished by its more triangular outline, the internal restriction and the different colour and pattern.

The range of *C. pseudoaurantius* overlaps with the range of *C. cedonulli* (here: *C. c. dominicanus*) between the N-coast of Grenada and Union Isle, a distance of about

50 km. This is the only case that 2 species of the *C. cedonulli* complex are geographically sympatric within a part of their range, but the species have not yet been found side by side on the same place. *C. pseudaurantius* seems to be confined to shallow water not deeper than 5 m, whereas *C. cedonulli* is most common in depths between 10 and 30 m.

#### III) Conus aurantius Hwass in Bruguière, 1792 (pl. 5, fig. 1-9)

- 1792 Conus aurantius Hwass in Bruguière, Encycl. meth. 1: 606; Tableau: pl. 317, fig. 7 (lectotype MHNG 1106/42)
- 1857 C. leucostictus Gmelin-Sowerby II, Thesaurus conchyliorum, 3. Conus: 7; pl. 189 [Conus, pl. 3], fig. 35, 36 (non Gmelin, 1791)
- 1958 C. dominicanus Bruguière-Coomans, Stud. Fauna Curaçao..., 8: 100; pl. 15, middle row, left fig. (non dominicanus Hwass in Bruguière, 1792)
- 1963 C. varius Linnaeus-Kohn, J. Linn. Soc. Lond. (Zool.), 44 (302): pl. 3, fig. 37 (see also Kohn, 1968: 442)
- 1968 C. aurantius Hwass-USTICKE, Carib. Cones...: 22 (No. 1012); pl. 3, lower row, 4th specimen wrongly marked "No. 1013 curassaviensis"
- 1970 C. aurantius Hwass-Clench & Bullock, Johnsonia 48: 375-376
- 1975 C. dominicanus Hwass-Humfrey, Seash. West Indies: 179; pl. 21, fig. 10
- 1976 C. aurantius Hwass-Kaicher, Card Catal., Pack 11: 1012
- 1977 C. aurantius Hwass-Lozet, Shells Caribbean: 98; fig. 159
- 1977 C. aurantius Hwass-Vink, Zool. Meded. 51: 88-89 [partim]; pl. 1, fig. 2, pl. 4, fig. 1-2
- 1979 C. aurantius Hwass-Walls, Cone Shells: 125 [partim]: lower left and lower middle
- 1981 C. aurantius Hwass-Coomans, Moolenbeek & Wils, Basteria 45: 31; fig. 159-160

T y p e: Muséum d'Histoire Naturelle, Geneva, lectotype MHNG 1106/42 selected by KOHN (1968) (pl. 5, fig. 1-2).

Locus typicus: "Philippines", corrected to Curacao (Netherlands Antilles, Caribbean Sea) by CLENCH & BULLOCK (1970: 375).

Description: Mean shell length 49.3 mm (S.D. = 7.9 mm, Range: 34.0-70.4 mm, N = 55). Body whorl relatively high in relation to shell height (mean relative diameter 0.61; morphometry see Table X). Spire rather short (pl. 5, fig. 6) to moderately elevated, straight-sided to very weakly concave-sided. Outline of body whorl straight or very slightly convex, its surface with granulated spiral threads, mainly near the base. Shoulder of the body whorl and spire whorls strongly coronated. Protoconch, when intact, sharply raised as a small knob on the more or less bluntly rounded first teleoconch whorls (pl. 12, fig. 10), a characteristic occasionally very weakly developed in C. pseudaurantius and not seen in any other member of the C. cedonulli complex. Aperture only very slightly broadening towards the base. No internal restriction on the anterior third of the columella within the aperture (see C. mappa). Colour purplish white with irregular large coalescing or occasionally isolated patches of orange, light brown, chocolate brown or black. Some specimens nearly completely coloured (pl. 5, fig. 7). On light areas numerous spiral lines of dark dots and dashes, on the dark areas — white dots, coinciding with the spiral threads and granules. Curacao specimens have golden brown or black patches (the brown often with dark outlines), Bonaire specimens have bright orange, golden brown, wine red or black patches, mostly without outlines. Inside of aperture white, in younger specimens outside colour showing through.

Specimens examined: Curacao: numerous specimens and various beach shells with faded colours from the SW-shore. Bonaire: numerous specimens and beach shells from the W-shore.

H a b i t a t: White coral sand with rubble and coral slabs, in 3-10 m, during the day normally found partly or completely buried in the sediment under coral heads or slabs.

Distribution: Endemic to Curacao and Bonaire, Netherlands Antilles.

D i s c u s s i o n: C. aurantius is easily distinguished from C. cedonulli, C. mappa and C. curassaviensis by its knobbed shoulder, the form of the protoconch and the early teleoconch whorls and the high body whorl. From C. pseudaurantius it is distinguished by its larger size, the larger and more pronounced shoulder knobs, the more narrow base and the denser and more numerous dark dots and dashes on the light background. In very large and old specimens of C. aurantius the knobs on the last half of the body whorl may become less pronounced or nearly obsolete. With up to 70 mm C. aurantius is the largest member of the C. cedonulli complex. Bonaire specimens show a greater variety in colour than specimens from Curacao. Coomans & al. (1981) report C. aurantius from Aruba, illustrating a beach shell from that locality. However, there are no records of live collected specimens yet, and contamination of the beach by material from Curacao or Bonaire cannot be excluded.

#### IV) Conus mappa Lightfoot, 1786

- 1786 Conus mappa Lightfoot, Catal. Portland Mus.: 116, No. 2554
- 1791 C. solidus Gmelin, Syst. Nat. ed. 13: 3389 (holotype ZMC)
- 1792 C. cedonulli mappa Hwass in Bruguière, Encycl. meth. 1: 602; Tableau: pl. 316, fig. 7
- 1942 C. dominicanus Hwass Clench, Johnsonia 1 (6): 6-8; pl. 4, fig. 4 (non Hwass in Bruguière, 1792)
- 1964 C. mappa Lightfoot Kohn, J. Linn. Soc. Lond. (Zool.), 45 (304): 162; pl. 2, fig. 18
- 1970 C. insularis Gmelin CLENCH & BULLOCK, Johnsonia 4 (68): 376-377; pl. 177, fig. 4 (non Gmelin, 1791)
- 1977 C. mappa Lightfoot VINK, Zool. Meded. 51 (5): 89-90; pl. 1, fig. 4, pl. 3, fig. 2, 4

T y p e: Specimen figured in KNORR (1757, pl. 8, fig. 4) selected by KOHN (1964) as representative of lectotype (pl. 7, fig. 4). Whereabouts of specimen unknown.

Locus typicus: "China", here corrected to Trinidad, Lower Caribbean. The locality "Les mers de l'Amérique méridionale" was already cited by HWASS for this "variété" of C. cedonulli.

Description: Mean shell length 46.0 mm (S.D. = 9.2 mm, Range: 27.1-66.5 mm, N = 47; morphometry see table XI). Shell heavy, with moderately elevated to high, straight-sided to more or less concave-sided spire and canaliculate whorls. Early whorls tuberculated, later whorls and body whorl with smooth shoulder. Body whorl straight-sided. Protoconch highly elevated, following teleoconch whorls more or less with the same steep slope, which in several specimens weakens towards the body whorl. Surface of the body whorl varying from smooth with faint spiral threads becoming stronger towards the base to more or less strongly granulated. Within the aperture on the inner part of the anterior third of the columella, there is a moderate to strong internal restriction, which can

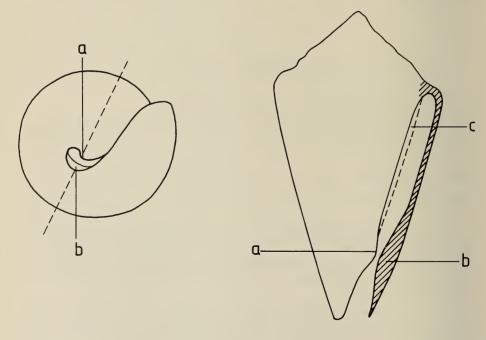
be seen when the shell is viewed from the base (pl. 8, fig. 9, pl. 9, fig. 11 and textfigs. 4-5). This "internal restriction" is a part of the outer shell layer which, during growth, is not dissolved in the same amount as the surrounding parts of the outer shell layer on the columella (textfig. 5).

Colour and pattern of *C. mappa* are quite variable. Shell whitish, pinkish white, purplish grey or even pale violet, with orange, yellowish brown or black spiral bands, mostly broken into more or less numerous irregular patches. In addition spiral lines of dark brown and white dots and short dark brown dashes. In some forms in the dark areas strings of white dots outlined with dark brown and interconnected by a thread of dark brown. Inside of aperture white to brownish or violet.

H a b i t a t: On silty sand or sand, both mineral or carbonate, from 3 to 80 m.

Distribution: On the continental shelf of the N-coast of South America between Santa Marta (Colombia) and Trinidad, also off the islands Los Testigos, Tobago and possibly Los Roques.

Discussion: C. mappa is most similar to C. cedonulli, but usually has a higher, often less concave and more stepped spire. The main distinguishing feature of C. mappa is the internal restriction within the aperture, only found in this species, and,



Figs. 4-5.

4: Basal view of *C. mappa granarius* from pl. 8, fig. 9, schematic drawing a: internal restriction; b: thickening of the interior of the outer wall; dotted line: line of the imaginary cut through the shell shown in fig. 5 (Drawing: M. Hänel); 5: Imaginary axial cut through a shell of *C. mappa granarius* to show situation of internal restriction (whorls omitted) a: internal restriction; b: thickening of the anterior part of the outer wall; c: already dissolved upper most layer of the inner wall (dotted line shows original outline) (Drawing: M. Hänel).

weaker, in C. curassaviensis. A thickening on the anterior part of the interior of the outer wall just opposite the position of the internal restriction on the columella is visible in all members of the C. cedonulli complex other than C. scopulorum, but its strongness and thickness is variable within each species (textfigs 4-5). In a study of the interior remodeling of the Conus shell, KOHN, MYERS & MEENAKSHI (1979: fig. 1) use the term "ridge" for this thickening of the outer wall; C. lividus Hwass in Bruguière, 1792, the subject of this study, has no internal restriction on the columella. — In some specimens of C. mappa the thickening on the inner side of the outer wall and the internal restriction on the columella come so close together that the remaining space in between is very narrow (pl. 9, fig. 11). In some very large specimens of C. cedonulli there is also found an internal ridge on the columella, but it never forms a considerable restriction of the aperture. On the other hand a few specimens of the Los Testigos population of C. mappa have been found with a very weak internal restriction only, but other specimens in the same population have the "normal" strong restriction. An internal restriction similar to that in C. mappa and C. curassaviensis has not yet been seen by the authors in other Conus species. Only the 10 specimens of C. zonatus Hwass in Bruguière, 1792 (Indian Ocean) studied, have a hint of an internal restriction, a fact already mentioned by Nybakken (1970a: 317: "the interior is ... partially obstructed by an internal ridge"). Although this ridge is not so strongly marked as in C. mappa, the space between this part of the columella and the inner side of the outer wall in C. zonatus is also very narrow. — From C. curassaviensis, C. mappa is distinguished by its larger size, the straight body whorl and the more strongly canaliculate whorls.

C. mappa is the representative of the C. cedonulli complex on the continental shelf of northern South America including some islands on the shelf. The 3 geographic subspecies show constant differences in colour and pattern. Within each subspecies higher spired deepwater forms exist.

A single live-collected specimen of a *Conus* belonging to the *C. cedonulli* complex (pl. 7, fig. 11) from Islas Los Roques (Venezuela) could not be identified with any species or subspecies dealt with in this report. Although most closely related to the *C. mappa* group because of the very strong internal restriction, it is distinguished by the widely spaced low, but visible knobs on the shoulder of the body whorl and a pattern of extremely close-set spiral lines of numerous very small dark brown dots. The colour of the shell is yellowish white with a few dark orange patches on the upper part of the body whorl, the inside of the aperture is white with a brownish rosy line at a distance of 2 mm from the margin. The specimen has been collected from sandy bottom within a Thalassia bed in shallow water. — Los Roques is separated by depths of 1800 m from the continental shelf of South America and the adjacent islands. — Because of lack of further material a taxonomic classification of this isolated population was not yet possible.

#### 1) Conus mappa mappa Lightfoot, 1786 (pl. 7, fig. 1-10)

Specimens examined: Trinidad: Morris Bay and off Monos Island, Bocas de Dragos, various specimens (pl. 7, fig. 2, 3, 6). Tobago: various specimens and fresh shells from the SW-coast (pl. 7, fig. 7-10).

H a b i t a t: In silty sand or silt and grit, mostly in flat areas, in about 15-40 m.

D i s t r i b u t i o n: Endemic to Trinidad and Tobago on the continental shelf of NE-South America.

Discussion: Typical *C. mappa* shells are milky white to pinkish white, with 2 spiral bands of greenish yellow to yellowish orange (Tobago) or brown to dark brown (Trinidad), broken into many irregular patches, flecks or spots. The body whorl has about 40 close-set spiral lines of dark dots on the light areas and white dots with dark outlines on the brown areas, interconnected by dark brown threads. The inside of the aperture is whitish. Some forms of *C. cedonulli cedonulli* have a quite similar pattern, but the spiral lines of white and brown dots are more close-set in *C. m. mappa* than in *C. c. cedonulli*, a difference already observed by Hwass (1792: 604). Some very large specimens from Tobago are extremely pale with light yellowish patches only. — The holotype of *C. solidus* Gmelin, 1791 (pl. 7, fig. 5) is without doubt a worn specimen of *C. m. mappa* from Trinidad.

#### 2) Conus mappa trinitarius Hwass in Bruguière, 1792 (pl. 6, fig. 6-13, pl. 8, fig. 1-2; 4, pl. 9, fig. 9)

- 1792 Conus cedonulli trinitarius Hwass in Bruguière, Encycl. meth. 1: 603; Tableau: pl. 316, fig. 2 (holotype MHNG 1106/59)
- 1792 C. cedonulli surinamensis Hwass in Bruguière, Encycl. meth. 1: 603; Tableau: pl. 316, fig. 9
- 1900 C. cedonulli Hwass-Dautzenberg, Mém. Soc. zool. Fr. 13: 162-163
- 1977 C. mappa Lightfoot-Vink, Zool. Meded. 51 (5): 89-91; pl. 3, fig. 3, 5
- 1977 C. cedonulli trinitarius Hwass-Kaicher, Card Catal., Pack 14: 1425 (holotype ill.)

T y p e: Muséum d'Histoire Naturelle, Geneva, holotype MHNG 1106/59 (pl. 6, fig. 7).

Locus typicus: "Océan Américain et c'est de l'Isle de la Trinité qu'on l'apporte ordinairement", here corrected to Islas Los Testigos, Venezuela.

S p e c i m e n s e x a m i n e d : Venezuela: Isla La Borracha (Estado Anzoategui), 2 specimens and various beach shells (pl. 8, fig. 2, 4); Islas Los Testigos, 8 specimens from shallow water (pl. 6, fig. 8-13), 1 shell from 80 m ("Chazalie" Sta. 26, DAUTZENBERG 1900: 162) (pl. 9, fig. 9), coll. IRSNB Bruxelles.

H a b i t a t: Silty sand or silt from 3 m (rare) to 10-20 m and deeper.

D i s t r i b u t i o n: Islands on the continental shelf area off the Eastern part of the coast of Venezuela.

D i s c u s s i o n: In C. mappa trinitarius the colour of the patches and maculations is quite variable from specimen to specimen, from black or orange to light greenish yellow. The patches are often not uniformly coloured and not darker outlined as in C. mappa mappa, but e.g. light brown with dark brown or yellowish with brown. A typical feature of various specimens of C. m. trinitarius, not seen elsewhere in the C. cedonulli complex is the presence of dark brown markings axially connecting some of the ochreous to orange brown patches and maculations and partially outlining a few patches (pl. 6, fig. 8), a characteristic already mentioned by Hwass (1792: 605) for C. c. surinamensis: "quelques traits d'un brun très foncé, qui ne se rencontrent pas dans les autres variétés". — In the numerous spiral lines the dark outlined white dots are very close-set or replaced by short dark brown and white streaks. The inside of the aperture is bluish white to pale violet.

From Hwass' illustration and description it is likely to assume that his *C. c. surinamensis* has originated from the *C. mappa* population of Eastern Venezuela. Hwass' erroneous type locality "Surinam" probably could be explained from the intensive trading contact between Surinam and Eastern Venezuela (Punta Araya) during the 17th and 18th century (see GOSLINGA 1971).

#### 3) Conus mappa granarius Kiener, 1848 (pl. 8, fig. 3, 5-11, pl. 9, fig. 1-8, 10-11, textfigs. 7-8)

- 1848 Conus granarius Kiener, Spec. Gen. Icon. Coquill. viv., Conus: 215; pl. 98, fig. 1
- 1879 C. catenatus Sowerby III, Proc. zool. Soc. Lond. for 1878: 796-797; pl. 48, fig. 3 (non Sowerby I, 1850)
- 1937 C. desmotus Tomlin, Proc. malac. Soc. Lond., 22 (4): 206 (nomen nov. for C. catenatus Sow. III, 1878)
- 1976 C. granarius Kiener-KAICHER, Card Catal., Pack 11: 1059
- 1977 C. cedonulli Linné-Dance & Cosel, Meeresmuscheln: 283 (2 specimens in lower row) (non Linné 1767)
- 1977 *C. sanctaemarthae* Vink, *Zool. Meded.* 51 (5): 91; pl. 1, fig. 5, pl. 4, fig. 4-6 (holotype RMNHL 55130)
- 1977 C. mappa Lightfoot-Vink, Zool. Meded. 51 (5): pl. 3, fig. 1
- 1977 C. cedonulli sanctaemarthae Vink-KAICHER, Card Catal., Pack 14: 1428
- 1977 C. granarius Kiener-Lozet, Shells Carib.: 110; fig. 201
- 1981 *C. consobrinus* Sowerby-Ретисн, *Malacologia* 20 (2): 332, 334, fig. 87-92 (non Sowerby I, 1850)
- 1983 C. cedonulli desmotus Tomlin-Coomans, Moolenbeek & Wils, Basteria 47: 97-98; fig. 381, 383

T y p e: coll. Bernardi (Kiener 1848). Specimen missing, apparently lost. Type figure in Kiener (1848: pl. 98, fig. 1) here reproduced (pl. 9, fig. 1).

Locus typicus: Not given, here selected Santa Marta, Dept. Magdalena, Colombia. South America.

S p e c i m e n s e x a m i n e d: Colombia: bays in the vicinity of Santa Marta, several specimens from 3 to 25 m (pl. 8, fig. 5-11), Aeropuerto Santa Marta, 20 m, 1 worn juv. shell; San Augustín-Dibulla, 50 m, 1 adult specimen (pl. 9, fig. 2); Manaure-Cabo de la Vela, 25-35 m, 4 adult specimens (pl. 9, fig. 5-8); Cabo Chichibacoa-Islas Los Monjes, 35 m, 1 juv. specimen (pl. 9, fig. 3) and 1 adult fresh shell (pl. 9, fig. 4). Venezuela: Golfo de Venezuela, ca. 30 m, 2 specimens (pl. 9, fig. 10).

H a b i t a t: On muddy sand, silt, fine sand or mixed sand both mineral or carbonate, often with calcareous algae and sponges, in shallow water occasionally on beds of *Zostera* or algae, from 3 to ca. 50 m, during the day partly or completely buried, sometimes under stones.

Distribution: North coast of South America from Santa Marta (Colombia) to Western Venezuela.

Discussion: The C. mappa granarius population comprises specimens with unusual colour and pattern not seen in other C. mappa subspecies. The ground colour is creamy white to pinkish white, pinkish grey, purplish grey or bluish violet. The patches or maculations are orange, yellowish brown, reddish brown or dark chocolate brown, sometimes reduced to narrow spiral bands only (see PETUCH 1981) or nearly missing, sometimes forming 2 broad bands more or less broken up into irregular patches like in the other subspecies of C. mappa. The specimens from the mineral substrate in the Santa Marta area have the typical purplish grey to bluish violet background and a bluish white to pale violet aperture. In some specimens the background colour looks darker than the light orange patches and maculations or spiral bands, a feature unique in the C. cedonulli complex. The specimens from coral or calcareous algae bottom usually have white, cream or pinkish white background with orange to reddish brown patches (see pl. 9, fig. 5-7) and a white aperture. The shape of C. m. granarius is considerably variable, from fairly broad with moderately high spire to slender with very high spire (deeper water specimens from off the Guajira Peninsula), juveniles of the slender form being nearly biconic. The surface is often strongly granulated, in fully grown individuals the granules may be less prominent or restricted to the anterior part of the shell (see also COOMANS 1973). The internal restriction is always strong to very strong (pl. 9, fig. 11).

The cones from the Santa Marta area and from the Guajira Peninsula exactly match the type figure in KIENER. Although the type locality is not given and the type specimen is unavailable, the extensive material studied in comparison with the type figure now allows the conclusion that *granarius* is the valid name for this subspecies, and Santa Marta is here selected as type locality. — The holotype of *C. desmotus* Tomlin (NMW, Cardiff) is a slightly worn, half grown specimen, which, in spite of the given type locality "Panama?", most probably originates from the Santa Marta area.

#### V) Conus curassaviensis Hwass in Bruguière, 1792 (pl. 10, fig. 1-10)

- 1792 Conus cedonulli curassaviensis Hwass in Bruguière, Encycl. meth. 1: 604; Tableau: pl. 316, fig. 4
- 1843 C. cedonulli Klein-REEVE, Conch. Icon., Conus, pl. 9, sp (fig.) 46, var. a and possibly var. c
- 1968 C. curassaviensis Hwass-USTICKE, Carib. Cones...: 22-23 (No. 1013), pl. 3 (lower row, third specimen, wrongly marked "No. 1012, C. aurantius")
- 1968 C. caracanus Hwass-Usticke, Carib. Cones...: 23 (No. 1013a), no figure (non Hwass in Brug., 1792)
- 1970 C. mappa Lightfoot-Holeman & Kohn, J. Conchol. 27: pl. 5, fig. 6 (non Solander in Lightfoot 1786)
- 1970 C. aurantius Hwass-Clench & Bullock, Johnsonia 48: 376, pl. 177, fig. 3 (non Hwass in Brug. 1792)
- 1976 C. aurantius Hwass form mappa Lightfoot-KAICHER, Card Catal., Pack 11: 1054
- 1977 C. insularis Gmelin-Vink, Zool. Meded. 51 (5): 89; pl. 1, fig. 3, pl. 2, fig. 4-6 (non Gmelin 1791)
- 1979 C. aurantius Hwass-Walls, Cone Shells: 159 (partim); 125 (fig. upper row and lower right) (non Hwass in Brug. 1792)

T y p e: Holotype missing, apparently lost. Type figure in LAMARCK (Tableau pl. 316, fig. 4) here reproduced (pl. 10, fig. 1).

Locus typicus: "Côtes de l'île de Curaçao", here corrected to Aruba, Netherlands Antilles.

Description: Mean shell length 41.9 mm (S.D. = 4.9 mm, Range: 31.4-51.0 mm, N = 55; morphometry see table XII). Spire moderately elevated to high and slightly concave-sided. Body whorl more or less convex-sided, surface with weak spiral threads near the base, but not granulated. Early whorls tuberculated, later whorls smooth and often somewhat canaliculate. Internal restriction on the columella weak to very weak, but always visible. Shells with yellowish brown, orange, reddish brown or black maculations or isolated patches on white background and fine spiral rows of white and brown dots and dashes placed close together. Background not always evenly white, but showing pale bluish and pinkish hues causing the dark areas often not being well delimited. Inside of aperture white.

Specimens examined: Aruba: Malmok, many specimens and empty shells.

H a b i t a t: Mostly carbonate sand and silt bottom with some vegetation, often under coral slabs, in shallow water (2-4 m).

Distribution: Endemic to Aruba, Netherlands Antilles.

D i s c u s s i o n: C. curassaviensis is most closely related to the C. mappa group, but it differs clearly by the distinctly convex body whorl, the smaller size, the less canaliculate whorls and the only weakly developed internal restriction. Furthermore the spire is slightly higher than in average C. mappa specimen from shallower water. In contrast to C. mappa, C. curassaviensis is a shallow water species and lives in a biotope more comparable to that of C. aurantius. From this species it is distinguished by its not so high and not granulated body whorl, the smooth shoulder of the last whorls, the higher spire and the more convex-sided body whorl. From C. pseudaurantius it differs by the not so high body whorl with smooth shoulder, the higher spire, the more close-set spiral lines of dots and dashes and the internal restriction. HWASS' description and figure of C. curassaviensis fit the Aruban species well, and e.g. the relatively smooth body whorl had already been pointed out ("...a une coquille plus lisse que les deux précédentes"... "mais les tubercules qui l'accompagnent y sont un peu moins exprimés". HWASS 1792: 604). His type locality "Curação" may have its origin from the fact that in the 18th and 19th century Curação was the main trading place of the Netherlands Antilles and that also shells from Aruba were exported via Curação.

Whereas Curacao and Bonaire with their *C. aurantius* populations are separated from Aruba and from the mainland by depths of about 1500 m, Aruba still lies on the continental shelf of the Paraguana Peninsula. Several Venezuelan mollusc species not found on Curacao and Bonaire occur on Aruba, and therefore it would have been obvious to deal with the Aruban population as a subspecies of *C. mappa*. On the other hand there exist various species endemic to Aruba only, e.g. *Conus hieroglyphus* Duclos, 1833, which often is found in association with *C. curassaviensis*. *C. curassaviensis* is more apart from *C. mappa* than the 3 *C. mappa* subspecies from one another, all distinguishing features are rather constant, and no intergrades have yet been found. The closest population of *C. mappa granarius* has been found near Los Monjes at a distance of about 60 km from Aruba. It cannot be fully excluded that *C. mappa granarius* also occurs closer to Aruba

in its adequate depth of 20-60 m and hence that geographic sympatricy with different biotopes is possible. Besides the constant distinguishing characters this is another support for considering *C. curassaviensis* as a full species, although sympatricy has not been proven yet.

#### VI) Conus consobrinus Sowerby I, 1850 (textfig. 6)

- 1850 Conus consobrinus Sowerby, Quart. J. geol. Soc. London, 6: 45
- 1928 Conus (Leptoconus) consobrinus Sowerby-Woodring, Carnegie Inst. of Washington Publ. 385: 214-215; pl. 11, fig. 6-7
- 1961 Conus consobrinus Sowerby- PFLUG, Acta Humboldtiana, Ser. Geol. Palaeontol. 1: 62; pl. 17, fig. 1-10

T y p e: British Museum (Natural History). Geological Department: holotype Geol. Soc. London No. 12803.

Locus typicus: Santo Domingo (Miocene) (Dominican Republic).

Description: See Woodring (1928) and Pflug (1961).

Distribution: Agueguexquite Formation (Mexico), Gatún Formation (Costa Rica and Panamá), Mare Formation (Cabo Blanco, Venezuela), Gurabo Formation (Dominican Republic), Bowden Formation (Jamaica) (after Petuch 1981: 334).

D i s c u s s i o n: The Miocene C. consobrinus could be an ancestor of the present C. cedonulli complex. It shows some similarities to the slender deepwater form of C. mappa granarius, but nevertheless is distinguished from the recent specimens from Guajira Peninsula by the following features: shoulder lower and rounded, spire whorls with pronounced spiral grooves just below the suture, but above the row of nodules, in the first (juvenile) whorls 4, then 3, and on the last part of the body whorl 2 grooves. In C. mappa granarius these grooves are missing, there are only faint spiral striae, overlain by growth lines. Weak spiral grooves are only noticeable on (?) and just below the shoulder, partly passing the nodules. The internal restriction of C. consobrinus is smaller, the thickening of the inner part of the outer wall is not directly opposite of the internal restriction, but more towards the spire. The curvation of the outer lip margin is in C. consobrinus slightly different, more gentle on the upper part than in most specimens of C. mappa granarius. In view of these differences, identification of the recent C. mappa granarius with C. consobrins cannot be supported.

#### VII) Conus archon Broderip, 1833 (pl. 9, fig. 12)

- 1833 Conus archon Broderip, Proc. zool. Soc. Lond. for 1833 (1): 54
- 1849 C. sanguineus Kiener, Spec. Gen. Coquill. viv., Conus: 356, pl. 111, fig. 2
- 1963 C. archon Broderip-Hanna, Occ. Pap. Calif. Acad. Sci. 35: 33-34; pl. 6, fig. 2, 6 (there more references)
- 1981 C. archon Broderip-Coomans, Moolenbeek & Wils, Basteria 45: 12; fig. 121

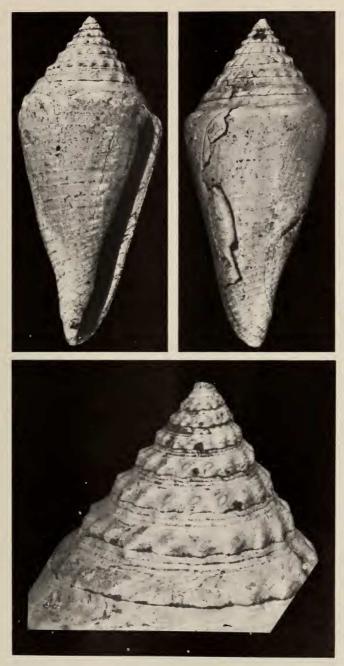


Fig. 6.

Conus consobrinus Sowerby I, 1850, 53 mm, Miocene, Dominican Republic, Gurabo Formation. Senckenberg Museum Frankfurt SMF (ex coll. Weyl) (Foto: R. Albert, courtesy R. Janssen).

T y p e s : British Museum (Natural History): 4 syntypes BM (NH) 1981 253, coll. Broderip.

Locus typicus: Bahía Montija, Pacific coast of Panama.

Description: See HANNA (1963) and WALLS (1979).

H a b i t a t: On sandy-silty and sandy bottom from about 3 m (rare) to 40 m or more.

Distribution: Gulf of California to Isla Gorgona (Colombia).

Discussion: C. archon is the Eastern Pacific cognate species to the Caribbean C. cedonulli complex and is most closely related to the C. mappa group. It is distinguished by the absence of the internal restriction, the smoother surface and the considerably smaller number of spiral lines with alternating white and brown dots and dashes, in some specimens being nearly obsolete. There is no colour variation of the brown patches and maculations, as in all Caribbean members of the C. cedonulli complex. A characteristic feature of adult C. archon is the strongly concave-sided spire with elevated early whorls and more flat later whorls. The animal is bright red like the animals of all other members of the C. cedonulli complex.

WALLS (1979) does not recognize that *C. granarius* is a subspecies of the Caribbean *C. mappa* and continues synonymizing this taxon with *C. archon*, although already HANNA (1963) had pointed out that *granarius* "is a synonym or variety of *cedonulli* of the West Indian region".

#### VIII) Conus scopulorum van Mol, Tursch & Kempf, 1971 (pl. 10, fig. 11-13)

- 1967 Conus dominicanus Hwass-VAN MOL, TURSCH & KEMPF, Annls Inst. océanogr. Monaco 45 (16): 244-245; pl. 9, fig. 3a-b (non Hwass in Brug., 1792)
- 1971 Conus scopulorum van Mol, Tursch & Kempf, Zool. Meded. 45 (15): 162, fig. 3-4; pl. 1, fig. 5-6
- 1976 C. scopulorum van Mol, Tursch & Kempf-KAICHER, Card Catal., Pack 11: 1044
- 1977 C. scopulorum van Mol-Lozet, Shells Caribbean: 110; fig. 202

T y p e s: Rijksmuseum van Natuurlijke Historie Leiden: holotype RMNH 8728 (Moll. alc.), 1 paratype RMNH 8729. Muséum National d'Histoire Naturelle Paris: 5 paratypes (3 of them broken into pieces). Museu Nacional Rio de Janeiro: 1 paratype.

Locus typicus: Ilha Fernando de Noronha, Brazil, 90 m.

Description: Shell small (up to 25 mm), with high to very high, straight-sided to slightly concave-sided spire. Body whorl very slightly convex-sided, surface with spiral threads, especially near the base. All whorls strongly tuberculated. No internal restriction on the columella. Shell white, with yellowish brown patches and maculations arranged in 2 broad bands. Instead of spiral lines of dots and dashes there are fine irregular axial and spiral lines, occasionally forming a pattern like the "brickwall" pattern in C. lucidus Wood, 1828 (Eastern Pacific) and C. boschi Clover, 1972 (Arabian Sea). Interior of aperture white. There is no variation in the colour of the patches.

H a b i t a t: Sandy and gravely bottom consisting of carbonate (calcareous algae) in deeper water (50-120 m).

Distribution: Endemic to the banks off Estado Ceará (Brazil) and the islands of Rocas and Fernando de Noronha.

D is c uss i on: C. scopulorum is least closely related to the other members of the C. cedonulli complex, and it is included here with reserve only. It is distinguished by its considerably smaller size, the strongly tuberculated whorls and the entirely different colour and pattern. The radula is also different (see Biological Notes).

From the *C. cedonulli* complex proper the population of *C. scopulorum* is isolated by a coastline distance of more than 2000 km and the biological barrier of the Amazone estuary system. It is therefore evident that *C. scopulorum* must have been separated from the *C. cedonulli* stock in the Caribbean at a very early stage, if indeed it originated from the same ancestor.

#### KEY TO THE RECENT MEMBERS OF THE Conus cedonulli COMPLEX

	Aperture of shell without internal restriction
	Aperture of shell with internal restriction on the inner part of the anterior third
	of the columella
1.	Shell 10-25 mm high, with high coronated spire, tuberculated shoulder and pat-
	tern with irregular minute vertical dashes in the white areas, distinct from all
	other cedonulli cones
1.	Shell 10-25 mm high, with high coronated spire, tuberculated shoulder and pat-
	tern with irregular minute vertical dashes in the white areas, distinct from all
	other cedonulli cones
	areas. Darker patches sometimes coalescing
2.	Body whorl slender in relation to height, slightly convex, with a knobbed shoul-
	der. Spire moderately high, nearly straight-sided
_	Body whorl broader in relation to height, with smooth and rounded shoulder,
	protoconch with nearly the same slope as the following teleoconch whorls, spire
	moderately high, mostly concave-sided, body whorl straight
3	Shell 50-70 mm high, granulated, protoconch sharply raised as a small knob on
	the bluntly rounded first teleoconch whorls, base not unusually broad, shoulder
	knobs pronounced
_	Shell 25-40 mm high, only weakly granulated, first teleoconch whorls less
	bluntly rounded, base broader and more rounded, spire shorter, shoulder knobs
4	smaller and less articulate
4	Shell with only few spiral lines and irregular often flame-shaped brown patches
	without much variation. Found only in the Eastern Pacific
	C. archon
_	Shell with close-set spiral lines of alternating dark brown dots and dashes,
	colour of irregular patches, maculations, bands or zones varies from yellow
	orange to black. Found only in the Caribbean
5	
5.	Shell 40-60 mm high, broad, moderately heavy, mahogany brown to black, with

irregular purplish white patches, zigzag markings or spiral bands, rarely uni-

form dark, light coloured areas small in relation to whole shell surface. Subre-Shell 40-60 mm high, broad, light to moderately heavy, yellowish white or pinkish rosy, with mostly isolated orange, brown or dark brown patches, the lighter orange ones always with darker outline. Light coloured areas large in relation Shell 40-60 mm high, broad, heavy to very heavy, bluish white with numerous small orange to brown patches, axial flames or zigzag markings, often coalescing spirally and arranged in 2 or 3 spiral bands. Patches usually not with darker Shell 30-50 mm high, internal restriction always weakly developed, body whorl markedly convex, spire high and straight-sided to slightly convex-sided, aperture Shell 40-65 mm high, internal restriction moderate to very strong, rarely weak, body whorl straight or near-straight, spire low to very high, straight-sided to concave-sided, aperture white or coloured within ..... Shell milky white, with irregular light greenish yellow to dark brown patches 7 and maculations, outlined with dark brown. White dots in spiral lines in dark areas outlined dark and interconnected by dark brown threads. Spire low to Shell whitish, with light yellowish green to black maculations and patches often not uniformly coloured and not consistently darker outlined. White dots in spiral lines very close-set or replaced by white streaks. Lighter brown or orange patches sometimes axially connected by dark brown markings. Aperture bluish white to pale violet. Internal restriction variable from strong to very weak. Spire low to moderately high, in deepwater specimens very high ... C. mappa trinitarius Shell whitish or purplish grey to bluish violet, with often only very few orange to dark brown patches or maculations, sometimes reduced to narrow spiral bands only. Surface more or less strongly granulated. Internal restriction always strong to very strong. Aperture white to pale violet or brownish. Spire modera-

#### III. BIOLOGICAL NOTES

#### ECOLOGICAL OBSERVATIONS, ALIMENTATION AND RADULAE

All members of the *Conus cedonulli* complex inhabit soft bottoms such as mineral (partly volcanic) sediment, carbonate sediment of coral or calcareous algae or a mixture of carbonate and mineral substrate. Grain size differs between silt and mixed sand with fine gravel and grit. In deeper water, the cones might also be found on muddy sand, but never on soft mud. In shallower water they are often associated with eel grass (*Thalassia, Zostera* etc.) or algae, and generally are confined to areas with secondary hard substrate like stones, rocks, coral heads and slabs, shells etc. In many localities they are also found in the vicinity of primary hard substrate such as the base of rocky shore or coral reefs and occasionally

even in larger sand patches on coral reef bottom. They never have been observed on the hard substrate itself except when laying eggs. *C. aurantius* and *C. curassaviensis* seem to prefer a slightly higher percentage of hard substrate than the other members of the *C. cedonulli* complex. In contrast to the superficially similar looking *C. regius* Gmelin, 1791, the cones of the *C. cedonulli* complex need calm water, and so they are mostly found in quiet bays, on the leeward side of islands or in depths well beyond the influence of the surf.

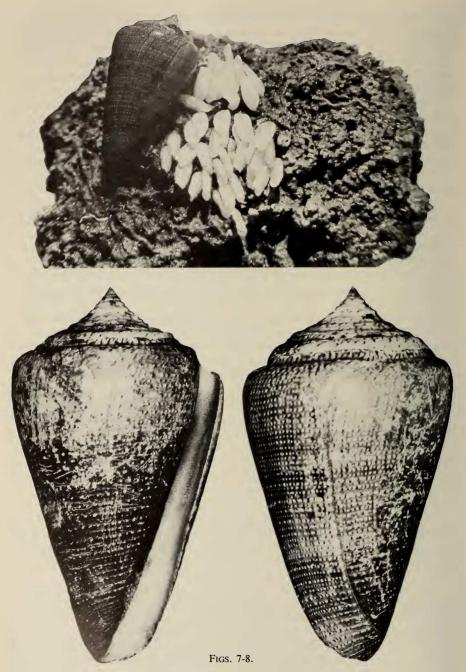
During day time, like most other species of *Conus*, they bury partly or completely in the sediment or hide under stones or other hard aggregates, where they normally are partly buried in the sediment underneath. At night they crawl around on the surface in search of prey (as observed in *C. archon*). Only very rarely a specimen is seen creeping in full daylight (one observation of *C. mappa granarius* in a *Zostera* field in Santa Marta, Colombia).

The known depth range is between 1,5 m and 160 m, but most specimens have been found between 5 and 40 m. Some species have a different depth preference.

Longer period observations on species of the C. cedonulli complex in their biotopes are only available for C. mappa granarius from the Santa Marta area. This subspecies normally prefers depths between ca. 15 and 35 m, and most of the few specimens found in more shallow water were not fully grown (a similar observation, juvenile specimens in more shallow water, has been made by VINK (1977: 83) on C. mappa mappa). Mating also takes place in the "usual" depths, as a pair collected in Santa Marta in 28 m while mating shows (specimens on pl. 8, fig. 5 and 6). 3 observations of C. mappa granarius lead to the assumption that for ovipositing the cones come to more shallow water. In August 1973 several adult specimens were found gathering on the underside of an old round concrete pole of a broken-down small boat jetty lying on the ground in a depth of 3 m (among them the specimen on pl. 8, fig. 9). A similar gathering in the same bay in about 2-4 m was found by the first author in July 1974 (VINK 1977: 82). At the end of June 1983 the Colombian biologist Juan DIAZ observed in another bay near Santa Marta several specimens laying eggs. On an area of ca. 10×3 m along the base of a coral reef slope in a depth of about 10-11 m he noticed more than 20 specimens and estimated about 1 specimen per m<sup>2</sup>. The cones were sitting on the sides or the undersides of small mineral stones scattered on the flat bottom consisting of mixed coral and mineral sand and grit with the alga *Udothea* sp. The eggs were attached to the undersides or sides of the stones (see textfig. 7-8) (DIAZ, personal communication). From these observations it can also be assumed that reproduction of C. mappa granarius in the Santa Marta area takes place mainly or exclusively during the summer months. — A congregation of C. cedonulli cedonulli with eggcases in shallow water was found on St. Vincent in October 1977 (D. HUNT, pers. comm.).

The cones of the *C. cedonulli complex* are worm-eaters and have the typical small, relatively short and broad radula teeth. VINK (1974) found *C. aurantius* eating a polychaete of the family Amphinomidae. The digestive tract of a *C. cedonulli cedonulli* from St. Vincent contained needles (setae) of a polychaete which also appeared to be an Amphinomid.

The venom apparatus is well developed, and there are no differences between the different species and subspecies so far as they have been dissected. The venom duct of a 50 mm specimen of *C. cedonulli cedonulli* measured 16,0 mm, the venom bulb had a length of 15 mm. The radula sac of a 47,7 mm specimen of the same species had a total length of 6,1 mm, the long arm (where the teeth are formed) measured 4,8 mm, the short arm (the sheath) 1,3 mm. In a *C. pseudaurantius* this sheath contained about 9-10 teeth ready-to-use (pl. 12, fig. 1-2). The radula teeth measured 1,2 mm in a 50,0 mm specimen of *C. c. cedonulli*.



7: C. mappa granarius Kiener beside egg cases on stone (just after collecting, near Santa Marta), June 1983. (Foto J. Diaz) (see p. 37); 8: A specimen of C. m. granarius collected on this occasion. Coll. J. Diaz. Ground colour violet with few dark bands; periostracum only partly removed. Natural size.

In comparison with the teeth of the amphinomid-eating cones C. zonatus Hwass in Bruguière, 1792, C. imperialis Linné, 1758 and C. brunneus Wood, 1828 (described and figured by Nybakken 1970a) and C. regius (cited by VAN MOL, TURSCH & KEMPF 1967), the teeth of the members of the C. cedonulli complex are generally more slender. With the teeth of the above mentioned species they have in common the small barb at the tip ("barb 1" in NYBAKKEN 1970b: 5, fig. 1), the barb at the end of the blade and the barb with the serration along its upper (outer) surface (in the position of NYBAKKEN's "barb 2"). This barb is only to be seen in teeth observed by light microscope with throughlight, but it is hardly or not seen on SEM micrographs, because the barb lies inside the hollow outlet for the poison formed by the blade, and it or its tip are often more or less covered by the external fold of the shaft just beside the blade barb (see KOHN, NYBAKKEN & VAN MOL 1972: fig. 1A and B). In the 4 amphinomid eating species mentioned above, this "internal" barb is situated at the same height of the tooth as the blade barb (C. regius, C. brunneus) or a little more behind it towards the base of the tooth (C. imperialis, C. zonatus). In the C. cedonulli group it lies slightly more towards the tip of the tooth, the tip of the "internal" barb is here situated at the base of the blade barb, so under certain circumstances it can be seen on SEM micrographs (pl. 11, fig. 4-6). In contrast to C. imperialis and C. zonatus, in C. regius and C. brunneus there is an additional accessory barb, which is situated on the back of the "internal" barb immediately behind the serration. This accessory barb more or less sticks out of the poison outlet (apical opening of the lumen). It is also present in the C. cedonulli group (pl. 11, fig. 2-6). The teeth of species of the C. cedonulli complex have one very weak spur on the base like in C. brunneus, while the teeth of C. zonatus and C. imperialis have 2 spurs (NYBAKKEN 1970a: 317).

The differences between the teeth of the different species and subspecies of the C. cedonulli complex other than C. scopulorum are minimal. The studied teeth of C. aurantius (pl. 11, fig. 1 i-j) seem to be slightly thicker than those of the other members of the C. cedonulli complex, and those of the studied C. cedonulli insularis from Barbados (deep water) (pl. 11, fig. 1 c-e) are more slender, but they are of exactly the same type, and therefore generally it seems not possible to distinguish between the entities of the C. cedonulli complex by means of the radula only. The teeth of the East Pacific C. archon are in size, shape and accessories similar to the Atlantic members of the C. cedonulli complex (see Nybakken 1970b: 8, fig. 9). The teeth of C. scopulorum have a quite similar lenght-width ratio, but the accessories are different: the blade is shorter in relation to the total tooth length, and, besides the small barb at the apex there is only "one strong tooth at the blade" (VAN MOL, Tursch & Kempf 1971: 165). This is another hint that C. scopulorum may have to be excluded from the C. cedonulli complex proper.

The general construction of the teeth with the typical accessories in comparison with the other amphinomid eating cones (presence and position of the "internal" barb, accessory barb and serrations together with the unornamented remainder of the shaft) as well as the rests of an amphinomid worm in the digestive tract of a *C. cedonulli cedonulli* and the observation of *C. aurantius* eating an amphinomid, prove that at least one considerable part of the regular diet of the cones of the *C. cedonulli* complex are polychaetes of the family Amphinomidae. So, besides the *C. regius-brunneus-bartschi* group and the *C. imperialis-zonatus* group, the *C. cedonulli* complex is the third *Conus* group known to feed on amphinomids.

A difference between the 2 other amphinomid-eating groups and the *C. cedonulli* complex is the biotope: The *C. imperialis* group as well as the *C. regius* group live on bottoms with a high percentage of hard substrate like coral reef platforms or edges, rocks etc.,

although they are usually found in sand pockets and patches within these areas. With the exception of *C. bartschi*, they prefer shallow water in the influence of surf or currents. The *C. cedonulli*-complex members, however, live in calm waters and are usually found on bottoms with smaller portions of hard aggregates (see above). From these ecological considerations and the different radula teeth, it can be assumed that the *C. cedonulli* group and the other 2 groups feed on different species or species groups of amphinomids, typical for the respective biotopes.

#### DEVELOPMENT

Among the Caribbean cones with known development, BANDEL (1975: 83-85; 1976: 183-187) cites *C. regius, C. mus* Hwass in Brug., 1792 and *C. ermineus* Born, 1778 as having a planctonic veliger stage, *C. spurius lorenzianus* Dillwyn, 1817 (as «*C. largillierti*») with a veliconcha which is «able to crawl and to swim», and *C. puncticulatus* Hwass in Brug.,

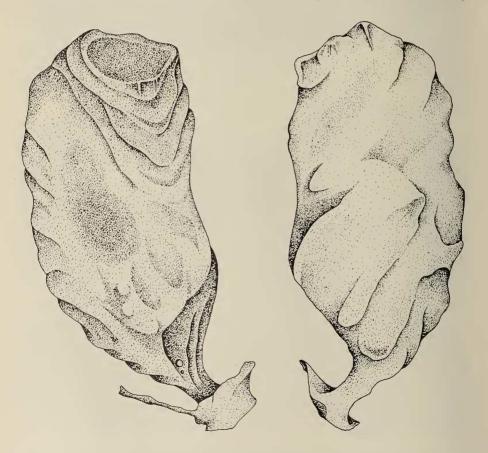


Fig. 9.

Egg case of C. cedonulli cedonulli, St. Vincent (Drawing: M. Hänel).

1792 (as «C. jaspideus pygmaeus») as a species where the young hatch as tiny snails which already have finished their development within the egg capsule. Of the C. cedonulli complex only 2 egg capsules of C. cedonulli cedonulli from St. Vincent and 2 capsules of C. c. dominicanus from the Grenadines were available for study (the capsules of C. mappa granarius contained fresh eggs only, J. DIAZ, pers. comm.). One egg case of each was opened. That of C. c. cedonulli contained 38 embryos in a capsule of 11,7 mm (inclusive the short peduncle) by 5,3 mm (textfig. 9). Of these embryos, 10 had a fully developed paucispiral embryonic shell with a length of 1,2-1,4 mm and a width of 0,7-0,8 mm, with a considerably long siphonal canal (pl. 12, fig. 3-7), while 17 embryos were medium-sized (0,8-1,0 mm length) with a smaller shell with only a siphonal notch, and 11 smaller ones (0,7 mm and less) were just in the process of forming the embryonic shell when the egg cases were collected. The youngs of C. c. dominicanus had already hatched, there was only one embryo left with fully developed shell of equal shape and size as C. c. cedonulli. Of the other members of the C. cedonulli complex it was only possible to study one protoconch of C. mappa granarius, one of C. aurantius (pl. 12, fig. 9-10) and one of C. pseudaurantius. The protoconchae have 1,5 whorls and a diameter of 0,7 mm. The other young and adult specimens at hand had all more or less eroded or broken protoconchae and could not be included in the study.

The number of embryos and the size of the embryonic shells resp. the protoconchae coincide most with the observation by BANDEL in *C. spurius lorenzianus* (1975: 85; 1976: 186-187). The egg capsules of this species contain 20-40 embryos, which hatch as veliconcha with an embryonic shell height of 1,3 mm. Comparing the numbers of embryos per capsule of the species cited by BANDEL (*C. ermineus*: 500 veligers, *C. mus*: 500-700 veligers, *C. regius*: 100-200 veligers, *C. spurius lorenzianus*: 20-40 veliconcha, *C. puncticulatus*: 9-21 crawling young) and their size and shape (see BANDEL 1975) with *C. c. cedonulli* allows the conclusion that, after having developed within their egg capsules, *C. cedonulli* and most probably all other members of the *C. cedonulli* complex lack a free swimming veliger phase and hatch at least in the late pediveliger (veliconcha) stage.

### IV. DISCUSSION

The Conus cedonulli complex is a typical example of a species complex with allopatric members which presumably have originated from a common ancester and which, after separation, have developed to species or subspecies. The various different populations as well as the many species names created since the times of LINNÉ (table XIII), often based on single specimens or very small lots only and in many cases without precise locality information or with the type specimen no longer available, made it rather difficult to establish a taxonomic scheme of the C. cedonulli complex.

The first task was the identification of specimens from a population in nature corresponding to the type, type figure or description of the various authors. Different nominal species which could be identified with specimens from the same population had to be considered synonyms. Different nominal species which were identified with specimens from separate populations were considered species or subspecies. In cases where the differences between these populations are not very pronounced, intermediates exist and the distribution ranges are adjacent, but not overlapping, a subspecific relationship was assumed. In cases where the two populations could be distinguished unambiguously and no intermedia-

tes were found to exist, and where the distribution ranges may be overlapping, separation on specific level was accepted.

In many cases, especially in the case of sibling species, the extent of morphological divergence is not always a measure for determining species or subspecies rank. We realize that our distinction between variability within a single species, subspecies diversity and separation on full specific rank may be considered somewhat arbitrary. KOHN (1980) and Lewis (1981) independently presented an objective methodology for distinguishing similar *Conus* species, and ideally one of these methods should have been used to test our conclusions. Unfortunately, however, the relative rarity of the cones of the *Conus cedonulli* complex makes it almost impossible to bring together large series from well defined localities for a generalizable statistical analysis; our situation is quite different from that of Lewis (1981), who studied the common indopacific *C. coronatus* Gmelin, 1791 and *C. aristophanes* Sowerby, 1857. Furthermore the methodologies cited above were not yet available when our project was started; throughout this study, of most specimens examined only shell length (SL), maximum diameter (MD) and in many cases aperture height (AH) were taken (SL, MD and AH as defined by KOHN & RIGGS 1975), and this allows objective morphometric analysis of these taxonomic characters only (tables VI, VIII-XII).

From the results of the measurements it is obvious that neither the width/length ratio (MD/SL) nor the relative diameter (RD=MD/AH) is acceptable as a single unique criterion for distinguishing between all species of the *C. cedonulli* complex. On the other hand, the measurements support the conclusion that e.g. the population from Aruba is quite distinct from those of Curacao and Bonaire. There is only a small overlap in the ranges of relative diameters, with most specimens of *C. curassaviensis* having RD above 0,64 and most specimens of *C. aurantius* with RD below 0,64. It is also shown that in general

TABLE VI
Summary of some mean morphometric parameters of 5 species of the Conus cedonulli complex (S.D. and regressions see tables VIII-XII)

C. cedonu	ılli	C. pseudaurantius	C. aurantius	С. тарра	C. curassaviensis
N	50	12	55	47	55
SL	47.1	34.5	49.3	46.0	41.9
W-L ratio (MD/SL)	0.53	0.49	0.48	0.53	0.50
N	38	12	54	45	54
RD=MD/AH	0.66	0.62	0.61	0.68	0.67

N = number of specimens SL = Shell length

W-L = Width-length

MD = Maximum Diameter RD = Relative Diameter

AH = Aperture Height

C. aurantius and C. pseudaurantius are more slender than C. cedonulli and C. mappa. The parameters MD/SL and RD are summarized in table VI.

Lewis (1981) recognized «shape» as a highly specific character and compared shells in outline (silhouette) with specimens of typical shape. In textfig. 10 characteristic shapes of the recent Western Atlantic cones of the *C. cedonulli* complex are shown. From the observation that *C. mappa* has a somewhat more triangular shape with a less concave more stepped spire than *C. cedonulli*, one would expect that the position of maximum diameter PMD and the rate of spire translation ST (as defined by KOHN & RIGGS 1975) would have been more significant parameters for distinction than the relative diameter, however, these were not measured. At any rate the easiest way to distinguish *C. mappa* from *C. cedonulli* is to establish the presence or absence of an internal restriction.

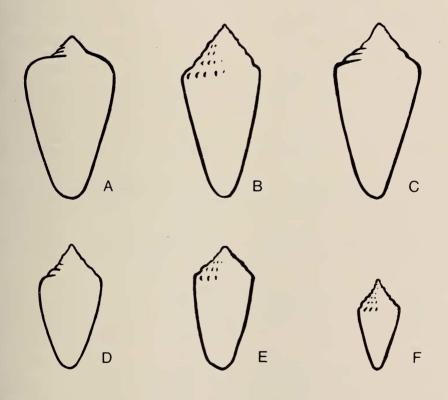


Fig. 10.

Characteristic shapes of recent Western Atlantic cones in the C. cedonulli complex (Drawing: Vink)

- A: C. cedonulli
- B: C. aurantius
- C: C. mappa
- D: C. curassaviensis
- E: C. pseudaurantius
- F: C. scopulorum

The development of the C. cedonulli complex cones (see above) gives further support to the hypothesis of a species complex with mostly allopatric members at various stages of speciation presumably originating from a common ancestor. The larvae of the cones of the C. cedonulli complex hatch at least in the late pediveliger stage, and so they are not able to cross e.g. areas of deep water. This has led to disjunct populations within the limits of the range area of the C. cedonulli complex in the Southern Caribbean. Besides the deep water channels separating populations in the Lesser Antilles and the Netherlands Antilles, there are also biological barriers along the north coast of South America for species with very short or without any pelagic veliger stage. One of these might be the very narrow continental shelf area with length of about 150 km near Caracas (Venezuela) without calm bays and probably without adequate environmental conditions. The large estuary of the Orinoco river with influence of brackish water may have been responsable for separate development of the Trinidad/Tobago population. The western distribution limit of the C. cedonulli complex coincides with a complex zoogeographical limit at the Caribbean coast of Colombia, which for most species is situated in the Santa Marta area. This limit separates cooler and very nutritive water with full salinity originating from upwelling east of Santa Marta from warmer, mostly turbid and sediment-charged water with often slightly reduced salinity southwest of Santa Marta (COSEL 1982; in print). The bottoms are also different: mineral sediments (fine sand to mud) along the mainland coast southwest of Santa Marta, mineral sand and mixed mineral and carbonate sediment in the Santa Marta area itself and the bays east of Santa Marta, a narrow shelf with coarse mineral sediment in the shallow and mud in the deeper part as far as San Augustin-Pedregal and vast areas of calcareous algae bottom along the Guajira coast from Dibulla to the Los Monjes area. Within the distribution limits of the Conus cedonulli complex there are still areas

without any record yet, but where members of the complex, even separate populations, can be expected. The recent "discoveries" of populations in Los Roques and Los Testigos support this view. On table VII all areas with their corresponding C. cedonulli complex populations (where present) and the depth ranges are summarized. Another separation, which is gradually proceeding, has taken place as a consequence of the rise of the Isthmus of Panama between Atlantic (Caribbean) and Panamic-Pacific populations. This raise took place during the Pliocene and was completed about 3,5 millions years ago (VERMEIJ 1978: 211). It is the only "time-mark" which clearly can be fixed in the development of the C. cedonulli complex, and which indicates the separation of C. archon from the remaining C. cedonulli stock. As speciation in gastropods in marine biotopes takes place very slowly, a number of the former amphi-american species has not yet achieved separate specific rank on both sides after the separation by the isthmus. Some are still not distinguishable and remain amphi-american (e.g. Architectonica nobilis Röding, 1789, Mazatlania aciculata (Lamarck, 1822), Anachis varia Sowerby, 1832) (see also VERMEIJ 1978: 213f), others may now be distinguished as subspecies (e.g. Purpura patula pansa Gould, 1853-P. p. patula Linné, 1759, Phalium granulatum centiquadratum (Valenciennes, 1852)-Ph. g. granulatum (Born, 1778)). A larger part, however, is treated in the literature as separate species (see lists in Vermeij 1978, and Cosel, in print), and also in the case of C. archon we can assume separation as a distinct species.

The separate development of *C. archon* allows us to evaluate the extent of morphological divergence which could have been achieved in the *C. cedonulli* complex within the defined period of 3,5 million years and which signalizes separation on specific level. Probably, with smaller differences between some distinguishable phena within the Caribbean *C. cedonulli* stock than between *C. archon* and the Caribbean stock, the time of phylogene-

TABLE VII

Localities within the area of distribution of the *Conus cedonulli* complex with populations and depth ranges (from West to East and from South to North)

Locality	C. cedonulli complex taxon recorded	Depth range
Columbia: Dept. Magdalena and La Guajira	C. mappa granarius	2-60 m
Venezuela: Estado Falcón (Golfo de Maracaibo)	C. mappa granarius	25-60 m
Venezuela: Estados Carabobo (Pto. Cabello), Aragua, Distrito Federal (La Guaira)	no record known	_
Venezuela: Estados Anzoategui (Pto. la Cruz), Sucre	C. mappa trinitarius	3-20 m
Trinidad, Tobago	С. тарра тарра	15-40 m
Aruba	C. curassaviensis	2- 4 m
Curação	C. aurantius	3-10 m
Bonaire	C. aurantius	3-10 m
Islas de Aves	no record known	_
Islas Los Roques	C. mappa (?)	5 m
Isla La Orchila	no record known	_
La Blanquilla and Islas Los Hermanos	no record known	_
Isla La Tortuga	"C. consobrinus" (Petuch, 1981) (= C. mappa)	65 m
Isla Margarita	no record known	<del>_</del>
Islas Los Testigos	C. mappa trinitarius "C. consobrinus" (Petuch, 1981) (= C. mappa)	10-15 m 70-80 m
Grenada: S- coast	C. pseudaurantius	3- 5 m
Grenada: NE-coast	C. cedonulli dominicanus	2-20 m
Carriacou: S-coast	C. pseudaurantius	3- 5 m
Carriacou: SW-coast	C. cedonulli dominicanus	2-20 m
Union Isle	C. pseudaurantius C. cedonulli dominicanus	3- 5 m 2-20 m
Cannouan	C. cedonulli dominicanus	
Mustique	C. cedonulli dominicanus	
Bequia	no record known	_
St. Vincent	C. cedonulli cedonulli	2-50 m
St. Lucia: W-coast	C. cedonulli cedonulli	(subrecent only)
St. Lucia: Gros Islet Bay	C. cedonulli insularis	20 m
Barbados	C. cedonulli insularis	160 m
Martinique and northward	no record known	_

tic divergence as a consequence of geographic separation was shorter for these phena than the known period of 3,5 million years. So, for example all distinguishable populations within *C. mappa* or *C. cedonulli* s. l. could be given subspecific rank only, and the 2 populations of *C. aurantius* (Curacao and Bonaire) were not at all separable.

For the taxonomic scheme of the known members of the *C. cedonulli* complex here presented, it is only possible to make typological decisions, based on morphological divergence ("morphospecies"). However, with the considerations discussed above, it has been tried to place the decisions against a more acceptable background rather than present these as unrelated and entirely subjective estimations, as has been a frequent practice in the past. Nevertheless it is remarkable that many of the forms in Hwass' arrangement coincide with the taxa here distinguished.

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### RESUMEN

Se presenta una historia de investigaciones anteriores del complejo *Conus cedonulli*, y se comentan los trabajos de Linné (1758 y 1767), Hwass (1792), Martini y Chemnitz (1773-1788), Schubert & Wagner (1829), Küster y Weinkauff (1837-1875), Reeve

(1843), KIENER (1845-1850), SOWERBY II (1857), MERMOD (1947) y VINK (1977). Dentro del complejo se distinguen 8 especies relacionadas: las especies recientes C. cedonulli Linné, 1767, C. pseudaurantius n. sp., C. aurantius Hwass in Bruguière, 1792, C. mappa Lightfoot, 1786, C. curassaviensis Hwass in Bruguière, 1792, C. archon Broderip, 1833, C. scopulorum van Mol, Tursch & Kempf, 1971, y la especie fossil C. consobrinus Sowerby I, 1850. C. cedonulli de las islas oceánicas del Caribe oriental (Antillas Menores) y C. mappa de la plataforma continental de Suramérica septentrional han desarrollado varias poblaciones distintas en las diferentes regiones geográficas. Estas poblaciones tienen diferencias constantes según color y dibujo, y por consecuencia están tratadas aquí como subespecies: C. cedonulli cedonulli, C. cedonulli insularis Gmelin, 1791, C. cedonulli dominicanus Hwass in Bruguière, 1792, C. mappa mappa, C. mappa trinitarius Hwass in Bruguière, 1792 y C. mappa granarius Kiener, 1848. Además existen variedades de color que fueron nombradas e.o. "C. caledonicus Hwass in Bruguière, 1792" y "C. holemani Usticke, 1968". Para cada taxon se suministran sinonimía, característicos de diferenciación e informaciónes sobre distribución y habitat. Se presenta un análisis de estadistica de los siguientes parámetros morfométricos: longitud de la concha (SL), diámetro máximo (MD) y altura de la abertura (AH).

Los miembros del complejo *Conus cedonulli* viven sobre fondos blandos salvo lodo y limo en la vecinidad de sustrato duro, entre 1,5 y 160 m de profundidad. Se alimentan sobre todo de poliquetos de la familia Amphinomidae.

Metamorfosis tiene lugar dentro de las cápsulas de huevos, los jovenes tienen una concha embrional paucispiral y salen por lo menos en el estado peciveliger final. No hay una fase planctónica.

El grupo de *C. cedonulli* es un complejo de especies y subespecies con miembros alopátricos, encontrándose en varios estados de especiación. Probablemente tienen su origen de un ancestro común, y ahora están separados por barreras biológicas.

### RÉSUMÉ

Le complexe de *Conus cedonulli* comprend 8 espèces apparentées: 7 espèces récentes, *C. cedonulli* L., 1767, *C. pseudoaurantius* n. sp., *C. aurantius* Hwass in Bruguière, 1792, *C. mappa* Lightfoot, 1786, *C. curassaviensis* Hwass in Bruguière, 1792, *C. archon* Broderip, 1833, *C. scopulorum* van Mol, Tursch & Kempf, 1971 et 1 espèce fossile, *C. consobrinus* Sowerby I, 1850. La partie historique de la présente étude retrace les étapes principales des recherches consacrées à ce groupe.

C. cedonulli des îles océaniques des Petites Antilles et C. mappa de la plateforme continentale septentrionale de l'Amérique du Sud ont développé des populations distinctes en différentes régions géographiques. Ces populations montrent des différences constantes de couleur et d'ornementation de la coquille et peuvent par conséquent être considérées ici comme des sous-espèces: C. cedonulli cedonulli, C. cedonulli insularis Gmelin, 1791, C. cedonulli dominicanus Hwass in Bruguière, 1792, C. mappa mappa, C. mappa trinitarius Hwass in Bruguière, 1792 et C. mappa granarius Kiener, 1848. De plus, des variétés de coloration ont également été nommées, par exemple "C. caledonicus" Hwass in Bruguière, 1792 et "C. holemani" Usticke, 1968.

Pour chaque taxon, nous avons précisé la synonymie, décrit en détail les caractères distinctifs et précisé les données actuellement disponibles sur la distribution et l'habitat. Nous

avons également effectué une analyse statistique des trois paramètres suivants: longueur de la coquille (SL), diamètre maximum (MD) et hauteur de l'ouverture (AH).

Les Cônes du complexe *cedonulli* vivent sur les fonds mous, à l'exception du limon ou de la vase, à proximité de substrats solides, entre 1,5 et 160 m de profondeur. Ils se nourrissent surtout de Polychètes de la famille des Amphinomidae.

La métamorphose a lieu à l'intérieur des œufs, les jeunes possèdent une coquille embryonnaire paucispiralée et éclosent au moins au stade pediveliger final. Il n'y a pas de phase planctonique.

Le groupe de *C. cedonulli* est constitué d'un complexe d'espèces et de sous-espèces dont les membres sont allopatriques et ont atteint des stades variables de spéciation. Ils dérivent très probablement d'un ancêtre commun et sont actuellement séparés par des barrières biologiques.

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## NOTES ADDED IN GALLEYS

- 1) It has not been possible to examine the specimens of *Conus* pictured by PETUCH (1981, figs. 87-92).
- 2) Publications after work on the manuscript of this study was completed:
  - COOMANS, H. E., R. G. MOOLENBEEK & E. WILS. 1985. Alphabetical revision of the (sub)species in recent Conidae 7. *cingulatus* to *cylindraceus*, including *Conus shikamai* nomen novum. *Basteria* 48 (6): 223-311 (treatment of *curassaviensis*).
  - VINK, D. L. N. & R. VON COSEL. 1985. Le complexe «cedonulli» (rapport intermédiaire),
     Xenophora n° 25: 11-14.

TABLE VIII Morphometric analysis of Conus cedonulli Linné, 1767

Shell length mm SL         Max. diam. mm MD         Apert. height mm AH         Width/ length ratio MD/SL         Rel. diam. RD = MD/AH         Origin         Illustration           56.2         29.2         44.8         0.52         0.65         St. Vincent St. Vincent MHNG 1104/90         Pl. 1, fig. 1 pl. 1, fig. 2           41.0         23.0         0.56         MHNG 1104/90         Pl. 1, fig. 4           45.3         27.5         0.61         MHNG 1104/88         Pl. 1, fig. 4           41.5         21.5         0.52         MHNG 1106/60         Pl. 1, fig. 6           44.8         23.4         35.7         0.52         MHNG 1106/60         Pl. 1, fig. 8           46.5         23.3         0.50         MHNG 1106/68         Pl. 1, fig. 19           49.4         28.2         43.1         0.57         0.65         St. Vincent         Pl. 1, fig. 12           60.5         32.0         0.53         BM(NH) 1969343         Pl. 2, fig. 2           61.5         33.2         50.5         0.54         0.66         St. Vincent         Pl. 2, fig. 2           47.3         25.6         38.3         0.54         0.67         St. Vincent         Pl. 2, fig. 5           49.0         24.8         39.1 <t< th=""><th>2</th></t<>	2
53.3         27.8         0.52         St. Vincent         pl. 1, fig. 2           41.0         23.0         0.56         MHNG 1104/90         Pl. 1, fig. 4           45.3         27.5         0.61         MHNG 1104/88         Pl. 1, fig. 5           52.7         28.6         44.2         0.54         0.65         St. Vincent         Pl. 1, fig. 6           41.5         21.5         0.52         0.66         St. Lucia (Castries)         Pl. 1, fig. 8           44.8         23.4         35.7         0.52         0.66         St. Lucia (Castries)         Pl. 1, fig. 8           38.7         19.0         31.0         0.49         0.61         St. Vincent         Pl. 1, fig. 12           49.4         28.2         43.1         0.57         0.65         St. Vincent         Pl. 1, fig. 12           60.5         32.0         0.53         0.53         BM(NH) 1969343         Pl. 2, fig. 2           47.3         25.6         38.3         0.54         0.66         St. Vincent         Pl. 2, fig. 4           40.4         20.4         33.1         0.50         0.62         St. Vincent         Pl. 2, fig. 5           49.0         24.8         39.1         0.51         0.63 <td>2</td>	2
1.0	2
1.0	2
45.3         27.5         0.61         0.61         0.65         MHNG 1104/88         Pl. 1, fig. 5           52.7         28.6         44.2         0.54         0.65         St. Vincent         Pl. 1, fig. 6           41.5         21.5         0.52         0.66         MHNG 1106/60         Pl. 1, fig. 6           44.8         23.4         35.7         0.52         0.66         St. Lucia (Castries)         Pl. 1, fig. 9           46.5         23.3         0.50         MHNG 1106/58         Pl. 1, fig. 9         Pl. 1, fig. 9           38.7         19.0         31.0         0.49         0.61         St. Vincent         Pl. 1, fig. 12           49.4         28.2         43.1         0.57         0.65         St. Vincent         Pl. 1, fig. 12           60.5         32.0         0.53         BM(NH) 1969343         Pl. 2, fig. 2         Pl. 2, fig. 3           61.5         33.2         50.5         0.54         0.66         St. Vincent         Pl. 2, fig. 3           47.3         25.6         38.3         0.54         0.67         St. Vincent         Pl. 2, fig. 4           49.0         24.8         39.1         0.51         0.63         St. Vincent         Pl. 2, fig. 5 </td <td>2</td>	2
52.7         28.6         44.2         0.54         0.65         St. Vincent         Pl. 1, fig. 6         Pl. 1, fig. 8         Pl. 1, fig. 8         Pl. 1, fig. 8         St. Lucia (Castries)         Pl. 1, fig. 9         Pl. 1, fig. 10         St. Vincent         Pl. 1, fig. 12         Pl. 1,	2
41.5         21.5         0.52         MHNG 1106/60         Pl. 1, fig. 8           44.8         23.4         35.7         0.52         0.66         St. Lucia (Castries)         Pl. 1, fig. 9           46.5         23.3         0.50         MHNG 1106/58         Pl. 1, fig. 12           38.7         19.0         31.0         0.49         0.61         St. Vincent         Pl. 1, fig. 12           49.4         28.2         43.1         0.57         0.65         St. Vincent         Pl. 1, fig. 12           60.5         32.0         0.53         BM(NH) 1969343         Pl. 2, fig. 2           61.5         33.2         50.5         0.54         0.66         St. Vincent         Pl. 2, fig. 3           47.3         25.6         38.3         0.54         0.67         St. Vincent         Pl. 2, fig. 4           49.0         24.8         39.1         0.51         0.63         St. Vincent         Pl. 2, fig. 6           48.8         26.0         41.0         0.53         0.63         St. Vincent         Pl. 2, fig. 7	2
44.8         23.4         35.7         0.52         0.66         St. Lucia (Castries) MHNG 1106/58         Pl. 1, fig. 9           38.7         19.0         31.0         0.49         0.61         St. Vincent         Pl. 1, fig. 11           49.4         28.2         43.1         0.57         0.65         St. Vincent         Pl. 1, fig. 12           60.5         32.0         0.53         BM(NH) 1969343         Pl. 2, fig. 2           61.5         33.2         50.5         0.54         0.66         St. Vincent         Pl. 2, fig. 3           47.3         25.6         38.3         0.54         0.67         St. Vincent         Pl. 2, fig. 4           49.0         24.8         39.1         0.51         0.63         St. Vincent         Pl. 2, fig. 6           48.8         26.0         41.0         0.53         0.63         St. Vincent         Pl. 2, fig. 7	2
46.5         23.3         31.0         0.50         MHNG 1106/58         Pl. 1, fig. 12           38.7         19.0         31.0         0.49         0.61         St. Vincent         Pl. 1, fig. 12           49.4         28.2         43.1         0.57         0.65         St. Vincent         Pl. 1, fig. 12           60.5         32.0         0.53         BM(NH) 1969343         Pl. 2, fig. 2           61.5         33.2         50.5         0.54         0.66         St. Vincent         Pl. 2, fig. 3           47.3         25.6         38.3         0.54         0.67         St. Vincent         Pl. 2, fig. 4           49.0         24.8         39.1         0.51         0.63         St. Vincent         Pl. 2, fig. 6           48.8         26.0         41.0         0.53         0.63         St. Vincent         Pl. 2, fig. 7	2
38.7         19.0         31.0         0.49         0.61         St. Vincent         Pl. 1, fig. 12           49.4         28.2         43.1         0.57         0.65         St. Vincent         Pl. 1, fig. 12           60.5         32.0         0.53         BM(NH) 1969343         Pl. 2, fig. 2           61.5         33.2         50.5         0.54         0.66         St. Vincent         Pl. 2, fig. 3           47.3         25.6         38.3         0.54         0.67         St. Vincent         Pl. 2, fig. 4           49.0         24.8         39.1         0.51         0.63         St. Vincent         Pl. 2, fig. 5           48.8         26.0         41.0         0.53         0.63         St. Vincent         Pl. 2, fig. 7	2
49.4         28.2         43.1         0.57         0.65         St. Vincent         Pl. 1, fig. 13           60.5         32.0         0.53         0.53         BM(NH) 1969343         Pl. 2, fig. 2           61.5         33.2         50.5         0.54         0.66         St. Vincent         Pl. 2, fig. 3           47.3         25.6         38.3         0.54         0.67         St. Vincent         Pl. 2, fig. 3           40.4         20.4         33.1         0.50         0.62         St. Vincent         Pl. 2, fig. 4           49.0         24.8         39.1         0.51         0.63         St. Vincent         Pl. 2, fig. 6           48.8         26.0         41.0         0.53         0.63         St. Vincent         Pl. 2, fig. 7	
61.5     33.2     50.5     0.54     0.66     St. Vincent     Pl. 2, fig. 3       47.3     25.6     38.3     0.54     0.67     St. Vincent     Pl. 2, fig. 4       40.4     20.4     33.1     0.50     0.62     St. Vincent     Pl. 2, fig. 4       49.0     24.8     39.1     0.51     0.63     St. Vincent     Pl. 2, fig. 6       48.8     26.0     41.0     0.53     0.63     St. Vincent     Pl. 2, fig. 7	
61.5     33.2     50.5     0.54     0.66     St. Vincent     Pl. 2, fig. 3       47.3     25.6     38.3     0.54     0.67     St. Vincent     Pl. 2, fig. 4       40.4     20.4     33.1     0.50     0.62     St. Vincent     Pl. 2, fig. 4       49.0     24.8     39.1     0.51     0.63     St. Vincent     Pl. 2, fig. 6       48.8     26.0     41.0     0.53     0.63     St. Vincent     Pl. 2, fig. 7	
47.3     25.6     38.3     0.54     0.67     St. Vincent     Pl. 2, fig. 4       40.4     20.4     33.1     0.50     0.62     St. Vincent     Pl. 2, fig. 5       49.0     24.8     39.1     0.51     0.63     St. Vincent     Pl. 2, fig. 5       48.8     26.0     41.0     0.53     0.63     St. Vincent     Pl. 2, fig. 7	
49.0 24.8 39.1 0.51 0.63 St. Vincent Pl. 2, fig. 6 48.8 26.0 41.0 0.53 0.63 St. Vincent Pl. 2, fig. 7	
49.0 24.8 39.1 0.51 0.63 St. Vincent Pl. 2, fig. 6 48.8 26.0 41.0 0.53 0.63 St. Vincent Pl. 2, fig. 7	
47.7 26.1 40.1 0.55 0.65 St. Vincent Pl. 2. fig. 8	
55.5 31.0 0.56 MHNG 1106/73 Pl. 3, fig. 1	
41.6 22.4 33.9 0.54 0.66 St. Vincent Pl. 3, fig. 3	
52.9 28.9 45.6 0.55 0.63 St. Vincent	
50.9 27.5 41.9 0.54 0.66 St. Vincent	
49.5 27.1 42.3 0.55 0.64 St. Vincent	
48.4 27.4 42.3 0.57 0.65 St. Vincent Vink (1977	) pl. 2, fig. 1
33.4 18.5 26.2 0.55 0.71 St. Vincent	
	) pl. 2, fig. 2
48.3   25.0   39.4   0.52   0.63   St. Vincent   Vink (1977	) pl. 1, fig. 1
47.0   25.6   37.0   0.54   0.69   St. Vincent	
49.4   27.0   41.8   0.55   0.65   St. Vincent	
54.3   30.2   45.8   0.56   0.66   St. Vincent	
40.5   20.6   31.3   0.51   0.66   St. Vincent	
32.2   16.5   25.2   0.51   0.65   St. Vincent	
43.0   22.1   33.7   0.51   0.66   St. Vincent	
48.2   25.5   38.2   0.53   0.67   St. Vincent	
53.4 30.0 42.5 0.56 0.71 St. Lucia (Pigeon I) Pl. 3, fig. 5	
50.1 26.3 40.5 0.52 0.65 St. Lucia (Pigeon I) Pl. 3, fig. 6	
47.0 23.5 0.50 MHNG 1104/92 Pl. 3, fig. 7	
42.5 21.1 33.8 0.50 0.62 St. Lucia (Reduit B) Pl. 3, fig. 8	
44.6 24.3 36.9 0.54 0.66 St. Lucia (Pigeon I)	
43.1 21.9 34.1 0.51 0.64 St. Lucia (Pigeon I)	
43.0 22.0 32.0 0.51 0.69 St. Lucia (Pigeon I)	
35.8 19.0 28.2 0.53 0.67 St. Lucia (Pigeon I)	
52.6 26.3 0.50 Barbados Pl. 3, fig. 9 55.3 27.6 0.50 Barbados Pl. 3, fig. 10	
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0.51	
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43.7 24.3 35.6 0.56 0.68 Carriacou Pl. 4, fig. 6 44.3 24.5 34.8 0.55 0.70 Carriacou Pl. 4, fig. 7	
71. 4, lig. 7	

Width/length ratio MD/SL:  $0.53 \pm 0.05$  (95% confidence, N=50)

Relative diameter RD = MD/AH:  $0.66 \pm 0.05$  (95% confidence, N=38)

Regression of shell length (SL) on maximum diameter (MD): SL = 1.62 MD + 6.48 (r=0.96, N=50) Regression of aperture height (AH) on maximum diameter (MD): AH = 1.51 MD + 0.33 (r=0.98, N=38)

TABLE IX Morphometric analysis of Conus pseudaurantius n. sp.

Shell length mm SL	Max. diam. mm MD	Apert. height mm AH	Width/ length ratio MD/SL	Rel. diam. RD= MD/AH	Origin	Illustration
29.9	14.7	23.3	0.49	0.63	Carriacou (S-coast)	Pl. 4, fig. 8
32.8	16.8	25.2	0.51	0.67	Grenada (paratype MNHNP)	Pl. 4, fig. 9
36.7	17.3	29.0	0.47	0.60	Grenada	Pl. 4, fig. 10
35.4	17.5	29.0	0.49	0.60	Grenada (subrecent)	Pl. 4, fig. 11
40.9	21.2	33.9	0.52	0.63	Grenada (subrecent)	Pl. 4, fig. 12
32.5	17.0	25.9	0.52	0.66	Grenada	Vink (1977), pl. 4, fig. 3
36.1	17.7	29.5	0.49	0.60	Grenada	
41.0	19.0	32.3	0.46	0.59	Union Isle	Pl. 6, fig. 5
34.5	17.4	28.0	0.50	0.62	Union Isle (holotype MHNG)	Pl. 6, fig. 1
31.5	15.7	25.6	0.50	0.61	Union Isle	Pl. 6, fig. 2
29.9	14.2	23.0	0.48	0.62	Union Isle	Pl. 6, fig. 3
33.0	16.5	26.9	0.50	0.61	Grenada (paratype MHNG)	Pl. 6, fig. 4

Width/length ratio MD/SL:  $0.49 \pm 0.04$  (95% confidence, N=12)

Relative diameter RD = MD/AH:  $0.62 \pm 0.05$  (95% confidence, N=12)

Regression of shell length (SL) on maximum diameter (MD):  $SL = 1.87 \text{ MD} + 2.62 \text{ (r=}0.87, N=}12)$ Regression of aperture height (AH) on maximum diameter (MD):  $AH = 1.72 \text{ MD} + 1.84 \text{ (r=}0.91, N=}12)$ 

TABLE X

Morphometric analysis of *Conus aurantius* Hwass in Bruguière, 1792

Shell   length   mm							
1.5	length mm	diam. mm	height mm	length ratio	diam. RD=	Origin	Illustration
44.2     20.6     32.9     0.47     0.63     Curação       34.8     16.7     26.7     0.48     0.63     Curação       46.2     22.1     36.3     0.48     0.61     Curação       51.5     25.4     39.4     0.49     0.64     Curação       45.3     21.8     34.3     0.48     0.64     Curação       36.1     17.6     27.9     0.49     0.63     Curação       57.7     27.7     44.8     0.48     0.62     Curação       45.2     21.7     33.6     0.48     0.65     Curação       48.7     24.0     38.2     0.49     0.63     Curação	49.5 56.0 64.2 63.0 51.5 58.3 45.5 48.5 55.6 49.6 52.6 47.6 43.2 47.3 55.6 47.0 57.1 70.4 63.3 57.1 45.8 52.6 52.3 51.6 52.3 51.7 45.2 51.7 45.2 47.4 39.3 40.8 47.9 49.3 40.8	24.0 27.2 30.1 27.4 25.8 28.4 22.2 27.2 22.8 24.5 22.3 20.3 22.9 25.0 21.6 27.4 27.0 21.9 25.2 24.7 24.7 24.7 24.7 24.7 24.7 25.1 21.3 22.3 18.4 20.1 17.0	44.5 49.2 46.5 42.8 46.9 36.6 36.1 45.8 38.3 41.4 36.8 32.9 43.0 35.7 44.3 55.1 49.2 44.3 43.6 34.2 41.7 40.4 39.7 46.2 35.4 39.6 36.1 37.6 39.3 31.9 29.2 28.8 31.7 37.7 37.7 37.7 36.2 38.3 37.9 37.9 38.3 38.3 38.3 38.3 38.3 38.3 38.3 48.3 48.3 48.3 48.3 48.3 48.3 39.4 37.4 48.3 37.7 37.8 37.9 44.8 37.8 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 37.9 44.8 37.9 44.8 37.9 37.9 44.8 37.9 47.9	0.48 0.49 0.47 0.43 0.50 0.49 0.48 0.49 0.46 0.47 0.47 0.47 0.48 0.45 0.46 0.48 0.49 0.47 0.47 0.48 0.49 0.47 0.47 0.48 0.49 0.47 0.47 0.48 0.49 0.47 0.47 0.48 0.49 0.47 0.47 0.48 0.49 0.47 0.47 0.48 0.49 0.47 0.47 0.48 0.49 0.47 0.48 0.49 0.47 0.49 0.47 0.48 0.49 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.47 0.49 0.47 0.49 0.47 0.49 0.47 0.47 0.49 0.47 0.49 0.47 0.47 0.49 0.47 0.47 0.49 0.47 0.47 0.49 0.47 0.47 0.49 0.47 0.47 0.49 0.47 0.49 0.47 0.47 0.49 0.47 0.47 0.49 0.47 0.47 0.49 0.47 0.47 0.49 0.47 0.47 0.49 0.47 0.49 0.47 0.47 0.49 0.46 0.46 0.46 0.47 0.47 0.47 0.49 0.46 0.46 0.47 0.47 0.49 0.46 0.46 0.47 0.47 0.47 0.49 0.46 0.46 0.47 0.47 0.47 0.49 0.46 0.46 0.47 0.47 0.47 0.48 0.49 0.46 0.47 0.47 0.48 0.47 0.47 0.48 0.47 0.47 0.49 0.46 0.47 0.47 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.48 0.49 0.48 0.48 0.49 0.48 0.48 0.49 0.48 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.49 0.48 0.48 0.49 0.48 0.48 0.49 0.48	0.61 0.61 0.69 0.60 0.61 0.61 0.64 0.59 0.60 0.59 0.61 0.62 0.65 0.61 0.62 0.64 0.60 0.61 0.62 0.63 0.63 0.63 0.63 0.63 0.60 0.61 0.69 0.61 0.69 0.61 0.60 0.61 0.60 0.61 0.60 0.61 0.60 0.63 0.59 0.63 0.61 0.64 0.60 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.61 0.69 0.63 0.61 0.64 0.63 0.64 0.64	Bonaire Curaçao Bonaire Curaçao Bonaire Curaçao Bonaire Curaçao	Vink (1977) pl. 1, fig. 2

Width/length ratio MD/SL:  $0.48 \pm 0.03$  (95% confidence, N=55)

Relative diameter RD = MD/AH:  $0.61 \pm 0.04$  (95% confidence, N=54)

Regression of shell length (SL) on maximum diameter (MD): SL = 1.99 MD + 2.73 (r=0.98, N=55)

Regression of aperture height (AH) on maximum diameter (MD): AH = 1.61 MD + 0.58 (r=0.99, N=54)

## Note:

Curação population only: MD/SL:  $0.48 \pm 0.03$  (95% confidence, N=26);

MD/AH:  $0.62 \pm 0.03$  (95% confidence, N=26);

Bonaire population only: MD/SL:  $0.47 \pm 0.03$  (95% confidence, N=28);

MD/AH:  $0.61 \pm 0.03$  (95% confidence, N=28).

TABLE XI

Morphometric analysis of *Conus mappa* Lightfoot, 1786

Shell length mm SL	Max. diam. mm MD	Apert. height mm AH	Width/ length ratio MD/SL	Rel. diam. RD= MD/AH	Origin	Illustration
56.2	33.1	45.2	0.59	0.73	Trinidad	Pl. 7, fig. 2
54.2	26.6	41.4	0.49	0.64	Trinidad	Pl. 7, fig. 3
51.0	29.0		0.57		Zool. Mus. Copenh.	Pl. 7, fig. 5
66.5	35.7	51.4	0.54	0.69	Trinidad	Pl. 7, fig. 6
37.9	20.2	29.6	0.53	0.68	Trinidad	Vink (1977) pl. 3, fig. 2
40.0	21.5		0.54		MHNG 1106/59	Pl. 6, fig. 7
41.0	22.3	33.5	0.54	0.67	Tobago	Pl. 7, fig. 8
58.8	30.6	44.1	0.52	0.69	Tobago	Pl. 7, fig. 7
48.1	25.5	39.8	0.53	0.64	Tobago	Pl. 7, fig. 9
50.9	29.4	40.9	0.58	0.72	Tobago	
51.1	28.1	39.6	0.55	0.71	Tobago	Pl. 7, fig. 10
53.0	29.0	43.3	0.55	0.67	Tobago	
37.7	19.7	29.3	0.52	0.67	Tobago	
46.3	23.9	36.2	0.52	0.66	Tobago	
52.8	27.5	42.3	0.52	0.65	Los Roques	Pl. 7, fig. 11
46.9	24.9	39.0	0.53	0.64	Isla Borracha	Pl. 8, fig. 2
27.4	13.8	22.0	0.50	0.63	Isla Borracha	
66.3	37.8	55.9	0.57	0.68	Isla Borracha	Pl. 8, fig. 4
50.0	27.6	41.1	0.55	0.67	Isla Borracha	
43.5	23.9	35.5	0.55	0.67	Colombia	Pl. 8, fig. 5
49.4	25.8	39.7	0.52	0.65	Colombia	Pl. 8, fig. 6
27.6	14.0	20.7	0.51	0.68	Colombia	Pl. 8, fig. 7
29.5	14.6	21.9	0.49	0.67	Colombia	Pl. 8, fig. 8
55.3	30.0	44.0	0.54	0.68	Colombia	Pl. 8, fig. 9
42.6	21.4	31.5	0.50	0.68	Colombia	Pl. 8, fig. 10
40.6	19.8	30.0	0.49	0.66	Colombia	Pl. 8, fig. 11
49.5	29.7	41.8	0.60	0.71	Colombia	
41.4	22.4	32.9	0.54	0.68	Colombia	Vink (1977) pl. 4, fig. 5
52.0	26.4	40.6	0.51	0.65	Colombia	
48.6	27.0	38.2	0.56	0.71	Colombia	Vink (1977) pl. 1, fig. 5
39.5	21.0	30.2	0.53	0.70	Colombia	
32.0	15.9	23.4	0.50	0.68	Colombia	Vink (1977) pl. 4, fig. 6
27.1	14.4	21.2	0.53	0.68	Colombia	DI O C 2
52.6	23.2	36.0	0.44	0.64	Colombia	Pl. 9, fig. 2
33.5	15.1	23.6	0.45	0.64	Colombia	Pl. 9, fig. 3
55.7	25.8	40.2	0.46	0.64	Colombia	Pl. 9, fig. 4
47.2 46.2	23.0	33.7	0.49	0.68	Colombia	Pl. 9, fig. 5
46.2	22.1 22.9	33.9 35.8	0.48	0.65 0.64	Colombia	Pl. 9, fig. 6
45.5	22.9	35.8	0.50	0.64	Colombia Colombia	Pl. 9, fig. 7 Pl. 9, fig. 8
56.9	27.3	41.6	0.52	0.69	Venezuela	1
48.3	26.8	36.5	0.48	0.00	Los Testigos	Pl. 9, fig. 10
50.4	26.8	38.4	0.50	0.73	Los Testigos Los Testigos	Pl. 6, fig. 8
46.5	26.0	36.5	0.52	0.08	Los Testigos  Los Testigos	Pl. 6, fig. 12
40.8	20.3	31.3	0.57	0.72	Los Testigos Los Testigos	Pl. 6, fig. 11 Pl. 6, fig. 10
38.8	20.1	28.8	0.53	0.72	Los Testigos  Los Testigos	Pl. 6, fig. 9
42.2	22.1	32.7	0.52	0.70	Los Testigos Los Testigos	Pl. 6, fig. 13
72.2	22.1	32.7	0.52	0.00	Los resugos	11. 0, 11g. 13

Width/length ratio MD/LS:  $0.53 \pm 0.07$  (95% confidence, N=47)

Relative diameter RD = MD/AH:  $0.68 \pm 0.05$  (95% confidence, N=45)

Regression of shell length (SL) on maximum diameter (MD): SL = 1.62 MD + 6.76 (r = 0.95, N = 47)

Regression of aperture height (AH) on maximum diameter (MD): AH = 1.16 MD + 7.93 (r=0.95, N=45)

TABLE XII

Morphometric analysis of *Conus curassaviensis* Hwass in Bruguière, 1792

Shell	Max.	Apert.	Width/	Rel.		
length	diam.	height	length	diam.		
mm	mm	mm	ratio	RD=	Origin	Illustration
SL	MD	AH	MD/SL	MD/AH		
51.0	25.2	20.7	0.50	0.65	A b -	DI 10 C - 2
51.0	25.3	38.7	0.50	0.65	Aruba	Pl. 10, fig. 2
47.5	22.5 20.0	30.1	0.47 0.50	0.66	BM(NH) 1969342 Aruba	Pl. 10, fig. 4 Pl. 10, fig. 5
39.9 47.5	23.4	35.8	0.30	0.65	Zool. Mus. Copenh.	Pl. 10, fig. 6
37.6	18.2	27.5	0.49	0.66	Aruba	Pl. 10, fig. 7
48.7	24.4	36.6	0.50	0.67	Aruba	Pl. 10, fig. 8
34.3	18.0	26.6	0.52	0.68	Aruba	Pl. 10, fig. 9
36.6	19.0	27.5	0.52	0.69	Aruba	Pl. 10, fig. 10
47.7	23.4	35.0	0.49	0.67	Aruba	- 11 10, 11g. 10
42.0	21.7	33.0	0.52	0.66	Aruba	
44.7	23.0	33.8	0.51	0.68	Aruba	
47.9	24.8	37.0	0.52	0.67	Aruba	Vink (1977) pl. 1, fig. 3
42.0	20.7	31.1	0.49	0.67	Aruba	Vink (1977) pl. 2, fig. 4
48.4	25.1	38.3	0.52	0.66	Aruba	Vink (1977) pl. 2, fig. 5
42.7	22.3	33.8	0.52	0.66	Aruba	Vink (1977) pl. 2, fig. 6
45.1	22.1	33.3	0.49	0.66	Aruba	
42.0	20.7	32.2	0.49	0.64	Aruba	
42.9	20.4	31.0	0.48	0.66	Aruba	
38.0	18.6	28.8	0.49	0.65	Aruba	
45.4	22.7	34.9	0.50	0.65	Aruba	
46.3	23.8	35.7	0.51	0.67	Aruba	
46.4 45.1	23.2	35.0	0.50 0.46	0.66	Aruba	
	20.9 16.9	33.0		0.63	Aruba	
32.7 36.3	18.4	25.0 27.6	0.52 0.51	0.68 0.67	Aruba Aruba	
34.1	17.2	26.0	0.50	0.66	Aruba	
45.2	22.6	33.4	0.50	0.68	Aruba	
43.9	22.5	32.4	0.51	0.69	Aruba	
45.5	22.9	35.3	0.50	0.65	Aruba	
37.0	19.6	28.2	0.53	0.70	Aruba	
37.5	18.4	28.4	0.49	0.65	Aruba	
44.6	21.8	33.1	0.49	0.66	Aruba	
47.3	23.3	35.5	0.49	0.66	Aruba	
39.5	20.1	30.4	0.51	0.66	Aruba	
46.2	23.2	35.7	0.50	0.65	Aruba	
41.6	21.5	31.2	0.52	0.69	Aruba	
38.4 46.3	18.4 25.0	26.8	0.48	0.69	Aruba	
34.6	17.6	36.2 26.3	0.54 0.51	0.69 0.67	Aruba Aruba	
43.0	20.9	32.8	0.31	0.67	Aruba	
39.5	20.0	30.6	0.49	0.65	Aruba	
45.9	23.6	34.7	0.51	0.68	Aruba	
44.5	21.8	33.2	0.49	0.66	Aruba	
38.0	18.9	28.4	0.50	0.67	Aruba	
35.1	17.6	26.5	0.50	0.66	Aruba	
46.5	23.0	34.6	0.49	0.66	Aruba	
35.0	17.8	26.8	0.51	0.66	Aruba	
39.5	19.0	29.4	0.48	0.65	Aruba	
48.5	23.2	34.2	0.48	0.68	Aruba	
39.0	19.4	29.1	0.50	0.67	Aruba	
37.8	18.6	28.0	0.49	0.66	Aruba	
43.5	21.7	33.0	0.50	0.66	Aruba	
37.4 31.4	18.9	28.6	0.51	0.66	Aruba	
39.6	16.1 19.7	23.5 29.6	0.51 0.50	0.69 0.67	Aruba	
37.0	17.7	29.0	0.50	0.07	Aruba	

Width/length ratio MD/SL:  $0.50 \pm 0.03$  (95% confidence, N=55)

Relative diameter RD = MD/AH:  $0.67 \pm 0.03$  (95% confidence, N=54)

Regression of shell length (SL) on maximum diameter (MD): SL = 1.95 MD + 1.08 (r=0.97, N=55)

Regression of aperture height (AH) on maximum diameter (MD): AH = 1.51 MD - 0.16 (r=0.98, N=54)

#### TABLE XIII

## Index of the taxa treated

amiralis Hw. in Brug., 1792 (form of cedonulli) archon Broderip, 1833 aurantius Hwass in Bruguière, 1792 caledonicus Hwass in Bruguière, 1792 caracanus Hw. in Brug., 1792 (form of cedonulli) catenatus Sowerby III, 1879 (non Sow. I, 1850) cedonulli Linné, 1767 consobrinus Sowerby I, 1850 curassaviensis Hw. in Br., 1792 (form of cedonulli) desmotus Tomlin, 1937 (nom. nov.f.catenatus Sow.) dominicanus Hw. in Br., 1792 (form of cedonulli) granarius Kiener, 1848 grenadensis Hw. in Brug., 1792 (form of cedonulli) holemani Usticke, 1968 insularis Gmelin, 1791 mappa Solander in Lightfoot, 1786 mappa Hw. in Brug., 1792 (form of cedonulli) martinicanus Hw. in Br., 1792 (form of cedonulli) nulli-secundus Usticke, 1968 pseudaurantius n. sp. sanctaemarthae Vink, 1977 sanguineus Kiener, 1848 scopulorum van Mol, Tursch & Kempf, 1971 solidus Gmelin, 1791 surinamensis Hw. in Br., 1792 (form of cedonulli) trinitarius Hw. in Br., 1792 (form of cedonulli)

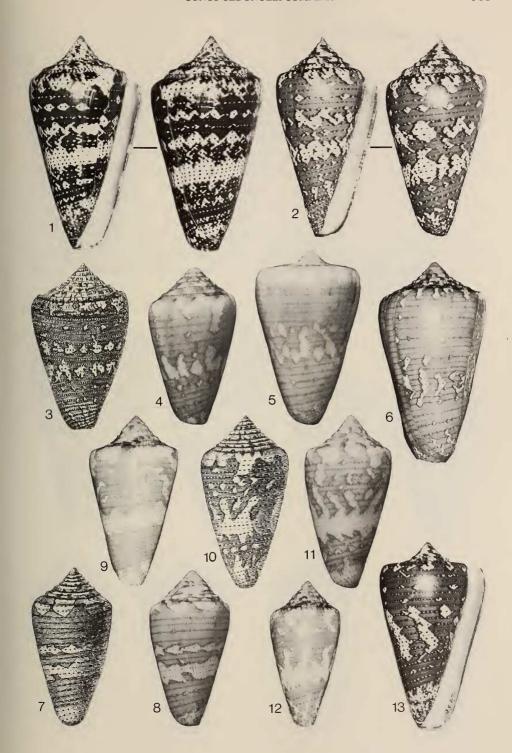
= cedonulli L., 1767 valid species valid species = cedonulli L., 1767 = cedonulli ?insularis Gmelin. 1791 = mappa granarius Kiener, 1848 valid species valid fossil species valid species = mappa granarius Kien., 1848 subsp. of cedonulli L., 1767 subsp. of mappa = cedonulli L., 1767 = cedonulli L., 1767 subsp. of cedonulli L., 1767 valid species = mappa mappa Lightfoot, 1786 = cedonulli L., 1767 = cedonulli L., 1767 valid species = mappa granarius Kien., 1848 = archon Broderip, 1833 valid species = mappa mappa Lightfoot, 1786 = mappa trinitarius Hw. in

subsp. of mappa Lightfoot, 1786

Brug., 1792

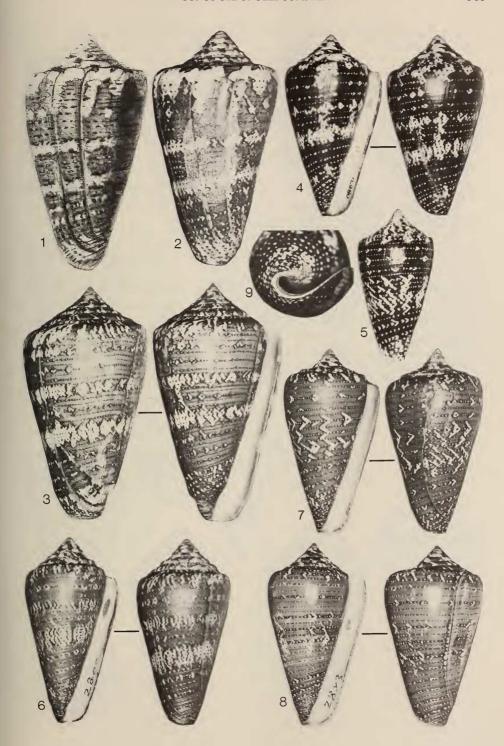
## PLATE 1 Conus cedonulli cedonulli L.

- 1) Conus cedonulli cedonulli L., St. Vincent, 5-6 m, sand and fine seagrass. leg. Hunt, coll. v. Cosel. Specimen with pattern more or less similar to the original illustration in Seba (see Dunn, 1971)
- 2) C. c. cedonulli L., St. Vincent, leg. & coll. Hunt
- 3) C. c. cedonulli L., Figure of C. cedonulli amiralis Hw. i. Br. in "Tableau", pl. 316, fig. 1
- 4) C. c. cedonulli L., Specimen MHNG 1104/90, ex coll. Lamarck
- 5) C. c. cedonulli L., Specimen MHNG 1104/88, ex coll. Lamarck
- 6) C. c. cedonulli L., St. Vincent, Kingstown harbour, dredge spoil, subrecent empty shell. leg. & coll. Vink
- 7) C. c. cedonulli L., Figure of C. cedonulli martinicanus Hw. i. Br. in "Tableau", pl. 316, fig. 3
- 8) C. c. cedonulli L., Holotype MHNG 1106/60 of C. cedonulli martinicanus Hw. i. Br.
- 9) C. c. cedonulli L., Castries, St. Lucia, harbour dredge spoil, subrecent empty shell. leg. Hunt, coll. Vink. Specimen similar to holotype of C. c. martinicanus Hw. i. Br.
- C. c. cedonulli L., Figure of C. cedonulli grenadensis Hw. i. Br. in "Tableau", pl. 316, fig. 5
- 11) C. c. cedonulli L., Holotype MHNG 1106/58 of C. cedonulli grenadensis Hw. i. Br.
- 12) C. c. cedonulli L., St. Vincent, Kingstown harbour, dredge spoil. leg. & coll. Vink. Specimen similar to holotype of C. c. grenadensis Hw. i. Br.
- 13) C. c. cedonulli L., St. Vincent, 10 m, sand. leg. Hunt, coll. Vink.



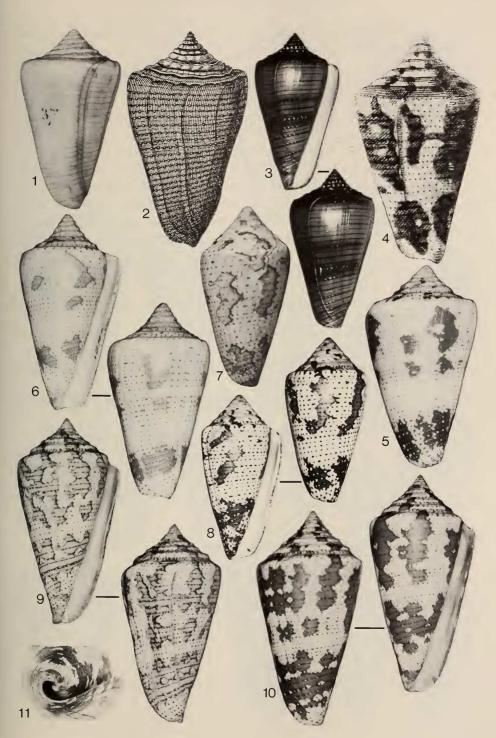
## PLATE 2 Conus cedonulli cedonulli L. (continued)

- 1) Conus cedonulli cedonulli L., Figure of "C. cedonulli Klein, var. d" in Reeve (Conus, pl. 9)
- 2) C. c. cedonulli L., Specimen BM(NH) 1969343 figured by REEVE (pl. 9, var. d)
- 3) C. c. cedonulli L., St. Vincent, fresh empty shell near octopus hole, 3 m. leg. Hunt, coll. v. Cosel. Specimen similar to the shell figured by REEVE (pl. 9, var. d)
- 4) C. c. cedonulli L. (black form), St. Vincent. leg. & coll. Vink
- 5) C. c. cedonulli L. (black form), St. Vincent. leg. Hunt, coll. Vink. Specimen similar to the shell figured by REEVE (pl. 9, var. e)
- 6) C. c. cedonulli L., St. Vincent, Young's Island. coll. Vink
- 7) C. c. cedonulli L., St. Vincent. leg. & coll. Vink. Specimen with zigzag markings, in certain aspects similar to the shell figured by REEVE (pl. 9, var. b)
- 8) C. c. cedonulli L., St. Vincent, leg. Hunt, coll. Vink. Specimen with very few white markings, forming a "transition stage" to the entirely dark "caledonicus" colour variety
- 9) C. c. cedonulli L., St. Vincent. leg. Hunt, coll. v. Cosel. Basal view to show that no internal restriction is present.



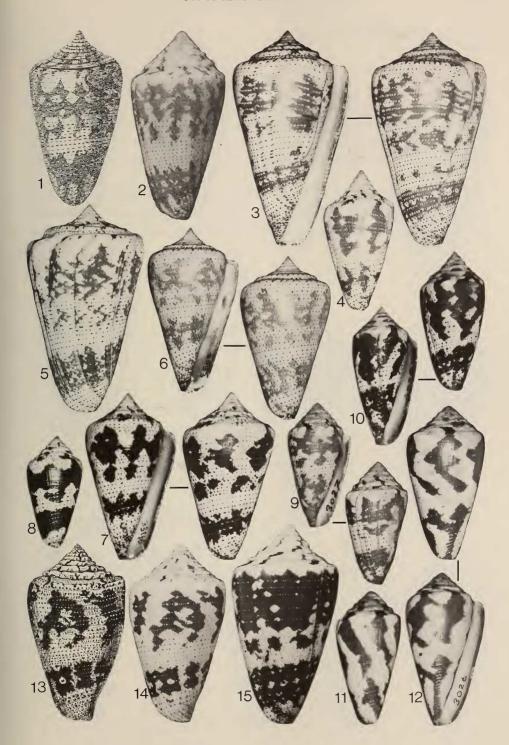
## PLATE 3 Conus cedonulli cedonulli L. (contd.)/Conus cedonulli insularis Gmel. Scale: natural size

- 1) Conus cedonulli cedonulli L., Holotype MHN 1106/73 of Conus caledonicus Hw. i. Br. (specimen faded)
- 2) C. c. cedonulli L., Figure of C. caledonicus Hw. i. Br. in "Tableau", pl. 321, fig. 10
- 3) C. c. cedonulli L., St. Vincent, leg. & coll. Hunt. Specimen of the uniform dark brown colour variety "caledonicus", similar to the holotype of C. caledonicus Hw. i. Br.
- 4) Conus cedonulli insularis Gmel., Representative of holotype of C. insularis Gmel. from Martini (1773, pl. 62, fig. 683), reproduced from Holeman & Kohn (1970)
- 5) C. c. insularis Gmel., St. Lucia, Pigeon Isle, dredge spoil. leg. & coll. Vink. Specimen with chestnut brown maculations more or less similar to the figure in MARTINI
- 6) C. c. insularis Gmel., St. Lucia, dredge spoil. coll. Vink
- 7) C. c. insularis Gmel., Specimen MHNG 1104/92, ex coll. Lamarck
- 8) C. c. insularis Gmel., Reduit Bay, St. Lucia, dredge spoil. coll. v. Cosel. Specimen similar to specimen MHNG 1104/92
- 9) C. c. insularis Gmel., off St. James, Barbados, 85 fms, sand with sponges, dredged coll. Hunt. Deep water specimen with extraordinary light coloured maculations
- 10) C. c. insularis Gmel., Barbados, same locality as specimen No. 9 coll. Hunt. Specimen with bright orange maculations
- 11) C. c. insularis Gmel., Specimen No. 10, view from underneath to show that no internal restriction is present.



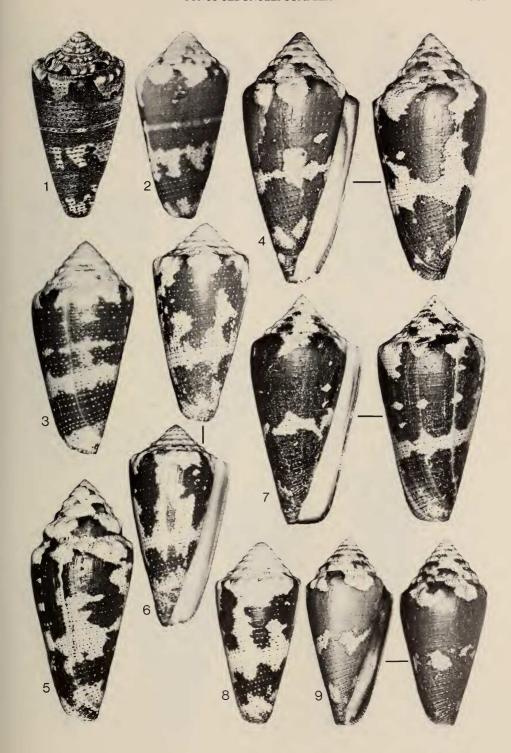
## PLATE 4 Conus cedonulli dominicanus Hw. in Br./Conus pseudaurantius n. sp./Conus cedonulli insularis (contd.)

- 1) Conus cedonulli dominicanus Hw. in Br., Representative of holotype. Reproduced from "Tableau", pl. 316, fig. 8
- C. c. dominicanus Hw. in Br., specimen MHNG 1104/89, apparently from Mustique, coll. Lamarck
- 3) C. c. dominicanus Hw. in Br., Mustique, Grenadines. Leg. & coll. Hunt
- 4) C. c. dominicanus Hw. in Br., Union Isle, Grenadines. Leg. & coll. Vink
- 5) C. c. dominicanus Hw. in Br., Palm Island, Grenadines. Coll. Vink
- 6) C. c. dominicanus Hw. in Br., Carriacou, Grenadines, 5 m, sand. leg. & coll. Vink
- 7) C. c. dominicanus Hw. in Br., same locality. Coll. Vink. Specimen with pattern resembling that of C. cedonulli caracanus Hw. in Br., but without the convex-sided body whorl
- 8) C. pseudaurantius n. sp., Paratype, Carriacou, Grenadines, south coast, 2 m, sand and coral, leg. & coll. Vink
- 9) C. pseudaurantius n. sp., Paratype MNHN Paris. Calivigny Island, Grenada, 1 m, coarse sand with coral, leg. Vink
- 10) C. pseudaurantius n. sp., Paratype, Calivigny Island, Grenada, 1 m, course sand with coral, leg. & coll. Vink
- 11-12) C. pseudaurantius n. sp., Ft. Jeudy Bay, Grenada, dredge spoil, subrecent empty shells, coll. Vink
- 13) C. cedonulli insularis Gmel., type figure in "Tableau" of C. c. caracanus Hw. in Brug., pl. 316, fig. 6
- 14) C. c. insularis Gmel., Holotype MHNG 1106/57 of C. c. caracanus Hw. in Br.
- 15) C. cedonulli L., Specimen MHNG 1104/93 (in coll. as C. c. caracanus Hw. in Br.), ex coll. Lamarck. No locality.



## PLATE 5 Conus aurantius Hw. i. Br.

- 1) Conus aurantius Hw. i. Br., Figure in "Tableau", pl. 317, fig. 7
- 2) C. aurantius Hw. i. Br., Lectotype MHNG 1106/42
- 3) C. aurantius Hw. i. Br., Bonaire leg. & coll. Vink
- 4) C. aurantius Hw. i. Br., Curacao leg. de Jong, coll. v. Cosel. Brown specimen
- 5) C. aurantius Hw. i. Br., Curacao leg. & coll. Vink. Exceptionally high, freak specimen
- 6) C. aurantius Hw. i. Br., Bonaire leg. Vink, coll. v. Cosel. Specimen with bright orange spots
- 7) C. aurantius Hw. i. Br., Curacao leg. de Jong & v. Cosel, coll. v. Cosel. Black specimen
- 8) C. aurantius Hw. i. Br., Bonaire leg. Vink, coll. v. Cosel. Chocolate brown specimen
- C. aurantius Hw. i. Br., Curacao leg. de Jong & v. Cosel, coll. v. Cosel. Brown specimen.



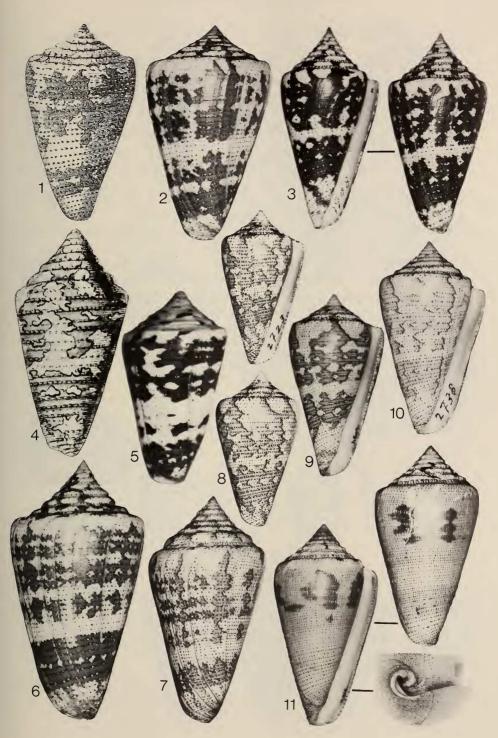
# PLATE 6 Conus pseudaurantius n. sp. (contd.)/Conus mappa trinitarius Hwass in Bruguière

- 1) Conus pseudaurantius n. sp., Holotype MHNG 983.991, Union Isle, Grenadines, 5 m, coral rubble and -sand
- C. pseudaurantius n. sp., Paratype, Union Isle, Grenadines, same locality as holotype. Coll. Vink
- 3) C. pseudaurantius n. sp., Paratype, same locality. Coll. v. Cosel
- 4) C. pseudaurantius n. sp., Paratype MHNG 975.428, Calivigny Island, Grenada, 1 m, coarse sand with coral. Leg. Vink. Black patches
- 5) C. pseudaurantius n. sp., Paratype, Union Isle, Grenadines, same locality as holotype. Coll. Vink
- 6) C. mappa trinitarius Hw. in Br., Figure of C. cedonulli trinitarius Hw. in Br. in "Tableau", pl. 316, fig. 2
- 7) C. mappa trinitarius Hw. in Br., Holotype MHNG 1106/59 of C. cedonulli trinitarius Hw. in Br.
- 8) C. mappa trinitarius Hw. in Br., Specimen similar to holotype, Islas Los Testigos, Eastern Venezuela, 10-20 m. Coll. Mailly
- 9-13) C. mappa trinitarius Hw. in Br., Islas Los Testigos, Eastern Venezuela, 0-20 m. 9-11, 13: coll. Vink; 12: coll. Mailly. Specimens with different colours:
  - 9): black markings on white
  - 10): bright orange markings on whitish
  - 11): black patches on bluish white
  - 12): pale yellowish olive green patches on pinkish white
  - 13): light greyish patches on whitish grey.



## PLATE 7 Conus mappa mappa Lightfoot/Conus ?mappa subsp. Scale: natural size

- 1) Conus mappa mappa Lightfoot, Figure of C. cedonulli mappa Hw. in Br. in "Tableau", pl. 316, fig. 7
- 2) C. m. mappa Lightf., Bocas de Dragos, Trinidad, 35 m, sand with silt. Leg. Percharde, coll. Vink. Specimen similar to the shell figured in "Tableau"
- 3) C. m. mappa Lightf., Morris Bay, Trinidad, 28 m. leg. Percharde, coll. Vink
- 4) C. m. mappa Lightf., Representative of lectotype of C. mappa Lightf. from Knorr (1757, pl. 8, fig. 4), reproduced from HOLEMAN & KOHN (1970)
- 5) C. m. mappa Lightf., Holotype of C. solidus Gmelin, Zoologisk Museum Copenhagen
- 6) C. m. mappa Lightf., Bocas de Dragos, Trinidad, 40 m. Leg. Percharde, coll. Vink
- 7) C. m. mappa Lightf., Tobago, 25-30 m, sand with rubble. Coll. v. Cosel
- 8) C. m. mappa Lightf., Tobago, 27 m, sand with coral. Leg. Vink, coll. v. Cosel
- 9-10) C. m. mappa Lightf., Tobago, same locality as preceding specimen. Leg. & coll. Vink
- 11) Conus ?mappa ssp., Islas Los Roques, Venezuela, shallow water, in Thalassia bed. coll. Vink.



# PLATE 8 Conus mappa trinitarius Hw. in Br. (contd.)/C. mappa granarius Kiener Scale: natural size

- 1) Conus mappa trinitarius Hw. in Br., Figure of C. cedonulli surinamensis in "Tableau", pl. 316, fig. 9
- 2) C. m. trinitarius Hw. in Br., Isla La Borracha, Eastern Venezuela, fresh empty shell, collected with hermit crab. leg. & coll. Vink
- 3) C. m. granarius Kiener, Holotype of C. desmotus Tomlin, National Museum of Wales, Cardiff
- 4) C. m. trinitarius Hw. in Br., Isla La Borracha, Eastern Venezuela, 3 m, sand. Leg. & coll. Vink
- 5-6) C. m. granarius Kiener, Santa Marta, Colombia, 28 m, sand with rubble. Leg. Erhardt, coll. v. Cosel. Specimens were mating when collected
- 7) C. m. granarius Kiener, near Santa Marta, 25 m, sand with rubble, dredged. Leg. & coll. v. Cosel. Juv. specimen with prominent granules over the entire shell
- 8) C. m. granarius Kiener, near Santa Marta, 2 m, coral sand, under coral slab. leg. & coll. v. Cosel. Specimen very light coloured with very few spots only
- 9) C. m. granarius Kiener, near Santa Marta, 3 m, mineral sand. Leg. & coll. v. Cosel. Specimen with orange flecks on violet. Basal view showing internal restriction
- 10) C. m. granarius Kiener, Santa Marta, 2 m, mineral sand. Leg. & coll. v. Cosel. Specimen with dark brownish bands
- 11) C. m. granarius Kiener, Santa Marta, 3 m, empty shell. Leg. & coll. v. Cosel. Specimen with chocolate brown bands.

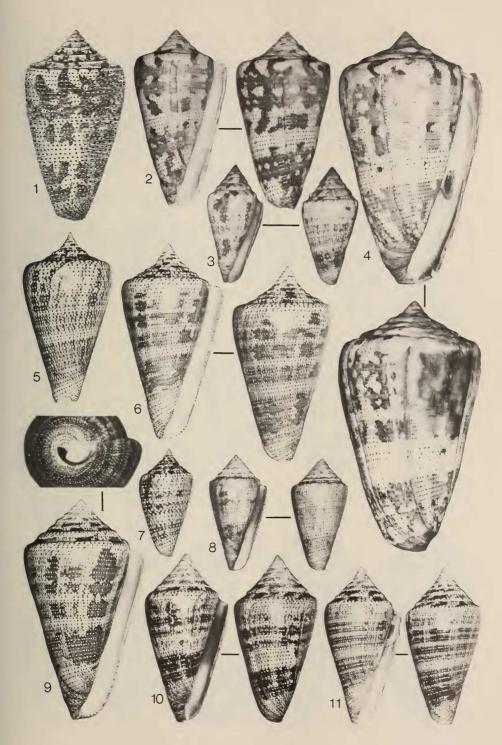


PLATE 9 Conus mappa granarius Kiener (contd.)/Conus mappa trinitarius Hw. in Br. (contd.)/Conus archon Brod.

- 1) Conus mappa granarius Kiener, Representative of holotype of C. granarius Kiener. Reproduced from KIENER (1848, pl. 98, fig. 1)
- 2) C. m. granarius Kiener, San Augustin-Dibulla, Colombia, 50 m, fine muddy sand, trawled, from shrimper. Coll. v. Cosel. Highspired deep water form
- C. m. granarius Kiener, Cabo Chichibacoa-Islas Los Monjes, Guajira, Colombia, 35-40 m, grey sand with calcareous algae, shells and sponges, trawled. Leg. v. Cosel, coll. Vink
- 4) C. m. granarius Kiener, Cabo Chichibacoa-Los Monjes, same lot as preceding specimen, crabbed empty shell, coll. v. Cosel
- 5-8) C. m. granarius Kiener, Manaure-Cabo de la Vela, Guajira, Colombia, 23-28 m, white carbonate sand and rubble with calcareous algae. Leg. & coll. v. Cosel
- 9) C. m. trinitarius Hw. in Br., Islas Los Testigos, Eastern Venezuela, 80 m, empty crabbed shell, dredged "Chazalie". Coll. IRSNB Bruxelles. A vermetid snail is attached to the shell (Foto: J. DARDENNE, courtesy J. VAN GOETHEM)
- 10) C. m. granarius Kiener, Golfo de Venezuela-Los Monjes, Venezuela, trawled, from shrimper. Coll. Vink
- 11) C. m. granarius Kiener, same specimen as No. 8, basal view to show the very strong internal restriction
- 12) Conus archon Broderip, Isla Gorgona, Pacific coast of Colombia, shore on the east side, 2 m, sand, fresh empty shell. Leg. & coll. v. Cosel.

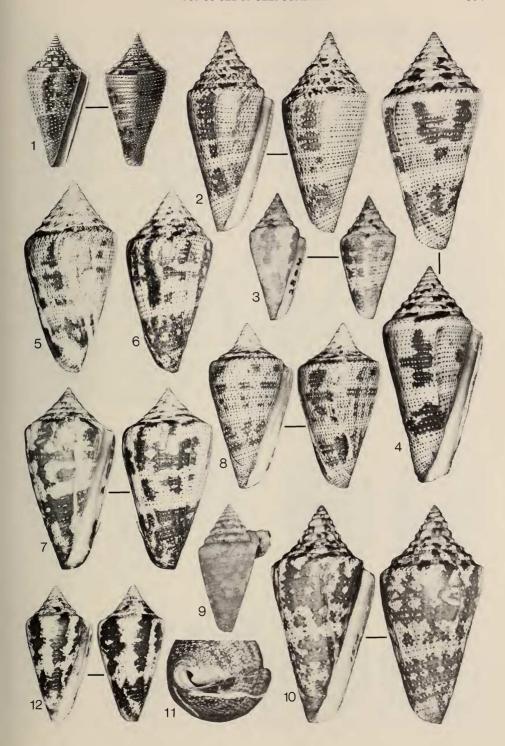
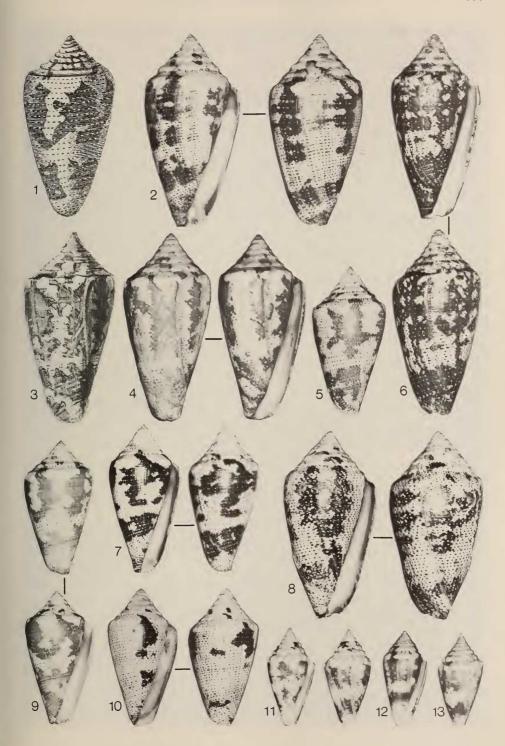


PLATE 10 Conus curassaviensis Hw. i. Br./Conus scopulorum van Mol & al. Scale: natural size

- 1) Conus curassaviensis Hw. i. Br., Representative of holotype of C. cedonulli curassaviensis Hw. i. Br. Reproduced from "Tableau", pl. 316, fig. 4
- 2) C. curassaviensis Hw. i. Br., Aruba, 2-3 m, sand, leg. & coll. Vink. Specimen quite similar to figure in "Tableau"
- 3) C. curassaviensis Hw. i. Br., Figure of "Conus cedonulli Klein var. a" in Reeve (Conus, pl. 9, fig. 46a)
- 4) C. curassaviensis Hw. i. Br., Specimen BM(NH) 1969342 figured by REEVE (pl. 9, fig. 46a)
- 5) C. curassaviensis Hw. i. Br., Aruba, leg. & coll. Vink. Specimen with pale brown pattern resembling that of the specimen figured in "Tableau", pl. 316, fig. 4
- 6) C. curassaviensis Hw. i. Br., Specimen from Zoologisk Museum Copenhagen, ex coll. Schnitgers, labelled "C. curassaviensis"
- 7) C. curassaviensis Hw. i. Br., Aruba, 2-3 m, sand, leg. Vink, coll. v. Cosel. Specimen with reddish brown pattern
- 8) C. curassaviensis Hw. i. Br., Aruba, leg. Vink, coll. v. Cosel. Very thick and stout specimen
- 9) C. curassaviensis Hw. i. Br., Aruba, leg. Vink, coll. v. Cosel
- 10) C. curassaviensis Hw. i. Br., Aruba, leg. & coll. Vink. Specimen with very few spots
- 11) Conus scopulorum van Mol & al., Fernando de Noronha, Brazil, coll. Kempf
- 12-13) C. scopulorum van Mol & al., same locality as specimen No. 11 coll. Vink.

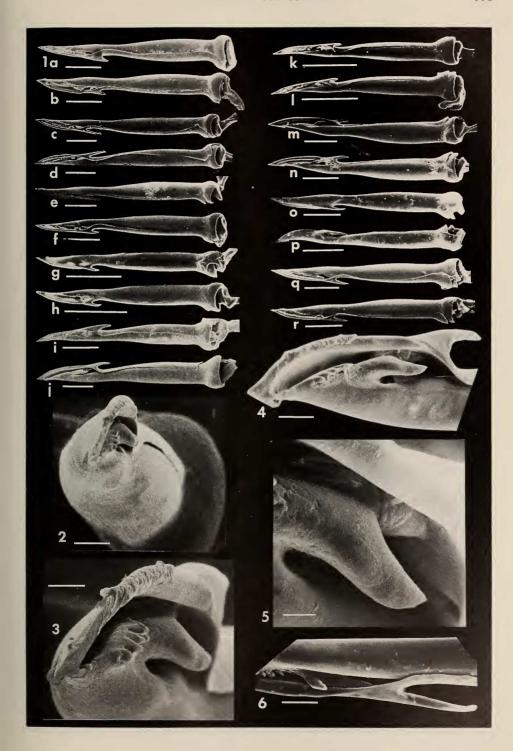


### PLATE 11 Radulae

- 1) Radula teeth of some cones in the Conus cedonulli complex
  - a-b) C. cedonulli cedonulli L., St. Vincent
  - c-e) C. cedonulli insularis Gmel., Barbados
  - f) C. cedonulli dominicanus Hw. in Br., Carriacou
  - g-h) C. pseudaurantius n. sp., Calivigny
  - i-j) C. aurantius Hw. in Br., Curação
  - k-l) C. mappa mappa Lightf., Tobago
  - m-n) C. mappa granarius Kiener, Santa Marta
  - o-p) C. mappa granarius Kiener, Dibulla
  - q-r) C. curassaviensis Hw. in Br., Aruba

## Scale: 200 µ

- 2) Apical view ("worm's-eye view") of a tooth of *C. aurantius* (same tooth as on fig. 1 j) to show the adapical opening, the accessory barb (compare with KOHN, NYBAKKEN & VAN MOL, 1972, fig. I c) and the external fold of the shaft. Scale: 40 μm
- 3) Same tooth, enlarged and slightly inclined to show adapical opening, serrations on the adapical portion of the inner fold and on the adapical portion of the external fold (blade or cutting edge) and accessory barb. Scale: 20 µm
- 4) Same tooth, more inclined to show adaptical opening with (from left) the small barb at the tip (apical barb), the second barb within the adaptical opening with the accessory barb in front of it, and the third barb or blade barb. Note unequal serrations in front of the accessory barb. Scale: 40  $\mu$ m
- 5) Same tooth, close-up view of second ("internal") barb and accessory barb. Scale: 10 µm
- 6) Close-up view of second barb with accessory barb and blade barb in the tooth of *C. cedonulli insularis* shown on fig. 1 e. Scale: 40 μm.



## PLATE 12 Radula sac and protoconchae

- 1-2) Conus pseudaurantius n. sp., Calivigny, short arm of radula sac (the sheath), opened with teeth ready-to-use in situ, lateral and apical view of teeth (one tooth accidently removed before preparation). Scale: 100 µm
- 3-7) *C. cedonulli cedonulli* L., St. Vincent, embryonic shell, removed from an egg case. Scale: 200 μm
- 8) Surface structure of the embryonic shell of C. cedonulli cedonulli. Scale: 30 µm
- 9) Protoconch and first teleoconch whorls of C. mappa granarius Kiener, Santa Marta. Scale: 1 mm
- 10) Protoconch and first teleoconch whorls of *C. aurantius* Hw. in Br., Curacao. Scale: 1 mm.

